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THE DIAPHRAGM IN MAN.

A RECORD OF OUR PRESENT KNOWLEDGE OF ITS DEVELOPMENT, RELATIONSHIPS, STRUCTURE, AND MODE OF ACTION.

BY

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I. INTRODUCTION.

"Where an organ can be diverted from one, and set to discharge another function, there Nature will spare herself the expense of forming a new organ, and will adapt the old one to a new use. She is prodigal in the variety of her adaptations. She is niggard in the invention of new structures" (Milne-Edwards).

In variety of functional adaptation the diaphragm among the other muscles takes prominent place. Nor is it solely of importance because of its several functions, but chiefly by reason of its central position. Midway between thorax and abdomen it touches and is touched by the chief *atria mortis*. Primarily a muscle concerned only with circulation, at a later developmental stage it has been put to many other uses, of which its action in respiration is the chief. In inspiration it enters into direct associate action with certain of the thoracic and spinal muscles; in expiration it is antagonised by the muscles of the abdomen; in deglutition it aids the buccal, pharyngeal, and œsophageal muscles; and in phonation, the laryngeal. These muscular actions are co-ordinated by means of neurons of association, whereby the nerves of the diaphragm are caused to enter into definite nerve-systems or combinations in order to effect the required movements. Primarily the abdominal musculature drove on the blood, the heart-force being expended chiefly in the gills; later, upon the introduction of lungs in connection especially with ribs and negative pressure, the abdominal wall also became respiratory; in the beginning, however, both diaphragm and body-wall were circulatory.

II. GENERAL VIEW OF THE FUNCTION OF RESPIRATION.

Respiration, being essentially organic, exists in the vegetable and animal worlds alike, its object being the intake of oxygen and the elimination of carbon dioxide. The chemical and mechanical methods by which these processes take place differ widely, being initiated in animals by invagination of epiblast derived from the digestive tract.

According to Darwin (1), all physiologists admit that "the swim-bladder is homologous or ideally similar in position and structure with the lungs of the higher vertebrate animals," and further, "in certain fish the swim-bladder seems to be nearly rudimentary for its proper function of giving buoyancy, but has become converted into a nascent breathing organ or lung" (2). Hence, since natural selection shows that there is no logical impossibility in this and other striking functional changes, it may be admitted that all vertebrates, at some period of their existence, have two distinct modes of breathing. In all vertebrates, gills or their representatives are present during embryonic existence; "in the fish and a few reptiles the gills are permanent, but in others they disappear, and, while traces of a lung are seen in all vertebrates, they acquire full development only in reptiles, birds and mammals; while again, certain amphibians, such as the proteus and siren, retain both gills and lungs to adult life, and thus form a link between fishes and reptiles" (3).

In the human embryo cephalic visceral clefts are present, the lowest three of these representing the gill-clefts of fishes and amphibia. In birds and mammals these clefts are not as a rule developed into complete apertures (4), and in Amniota appear to remain closed throughout fœtal life (5). "In some fishes the branchial arches and clefts are more numerous than in other vertebrates, and in a few the hyoid arch also develops a gill" (6). The fourth and fifth visceral arches may be considered to belong to the neck rather than to the head.

The simplest form of direct aëration of the blood by means of lung-structures is seen in reptiles which have large simple sacs into which the air is introduced by deglutition. In birds the apparatus is more elaborate, since the sacs are subdivided into lobules.

The mammalian respiratory system consists of:—

1. An osseous framework—the thorax.
2. Systems of opposing muscles—

(*a*) Inspiratory,
(*b*) Expiratory,
(*c*) Muscles of fixation.

3. Larynx, trachea, bronchi, and lungs.

"Mammals alone possess a perfect thorax, *i.e.* a closed cavity for the heart and lungs, with movable walls and a muscular partition, the diaphragm separating the thoracic from the abdominal cavity" ([7]).

III. THE MECHANISM OF RESPIRATION IN MAN.

"Accurate representations of the exterior and interior of the dead body give no adequate idea of the movements and varying position of those parts during life" (Sibson).

In order clearly to understand the nature of the events which take place during the different phases of the respiratory cycle it is necessary to broaden one's outlook and to regard the mechanism of respiration as influencing, and, in turn, being influenced by, the whole structure of the organism. Any variation in the contour of the trunk produced by muscular action, or any change in size of the body-cavity, produces a definite and corresponding effect upon respiration. All the other systems influence to some degree the character of the respiratory movements, especially the nervous system in conscious or subconscious action.

No conception has hindered our progress in respiratory mechanics so much as that which for centuries has figured the body-cavity as divided into two compartments by a "transverse septum"—the diaphragm. This half-truth is more misleading than the worst falsehood.

The clearest idea of the mechanism of respiration is probably gained by regarding man from the comparative standpoint, and his abdominal and thoracic cavities as together constituting one cœlom; the diaphragm being considered as a structure subsequently introduced within the body-cavity, primarily in order to aid the flow of blood, and secondarily to play its part as a respiratory muscle. On reviewing this aspect of the case we see that the influence of respiration prevails in continuity throughout the body-cavity, the whole of the contents being acted upon by the movements of breathing, and the regional effects of these being manifest from neck above to perineum below.

The study of the mechanism of respiration is essentially difficult inasmuch as fixation of any given portion of the trunk is merely relative. Even the vertebral column, which has been almost universally considered the one portion of the body which is fixed during respiration, although it is more immobile than any other part of the thorax, yet is not a fixed structure, but is subject to variation in position according to the stress of the particular moment[8]. Hence it is not surprising that, throughout many centuries, all kinds of conflicting opinions have been put forward as to the precise movements that occur, and as to the interpretation of their results.

Further, confusion of thought has resulted from the fact that details of the respiratory mechanism have been considered by themselves without regard to their value in the general economy. Thus it is a matter of experience that, clinically, respiration not infrequently is regarded solely from the thoracic standpoint, whilst the equally important part played by the abdominal muscles is overlooked; the abdomen being examined solely with reference to the soundness or otherwise of the contained viscera without regard to their movements during the respiratory cycle.

It is impossible to dissociate the action of the diaphragm from that of the other thoracic, spinal, and abdominal muscles, since its mediate position causes it to share in their action, and thereby to show how the movements of each great group are correlated. Hence the abdominal muscles must be studied equally with those of the thorax, which have up to now engrossed too large a share of attention, and these, in turn, together with those of the vertebral column. Respiration is not solely a thoracic act; each time we breathe quietly our abdominal muscles are called into play equally with our thoracic muscles, and in deep respiration this is still more evident. In the female sex, possibly owing to the use of corsets, the outward action of the abdominal muscles has been checked; but the respiratory movement, although slight, is still seen.

At the outset it is of the highest importance to recognise the fact that, from beginning to end, the respiratory cycle depends in greatest measure upon muscular action. Thus in inspiration elevation of the ribs occurs with coincident extension of the vertebral column and pushing outwards of the anterior abdominal wall; in expiration, contraction of the abdominal wall with lowering of ribs and forward movement of vertebral column. Some effect, it is true, is due to elastic recoil dependent upon change in position of bones, ligaments, and soft parts; but this, of itself, has far less influence, and is merely secondary to the definite effects produced by the contraction of muscles.

IV. THE DIAPHRAGM.

A.—ORIGIN AND DEVELOPMENT.

"The individual organism recapitulates in its own developmental history the several stages through which its ancestors passed in their evolution" (Kowalewsky).

In dealing with the development of the diaphragm I shall follow in the main the views which have been so ably put forward by Dr. Arthur Keith in his researches into the nature of the mammalian diaphragm and pleural cavities, which views, as I believe, afford the fullest and most satisfactory explanation yet advanced.

1. *Evidence Derived from Comparative Anatomy.*

By employing the comparative method of investigation, we arrive at the following three stages in the developmental history of the diaphragm. In fishes and amphibians the septum transversum divides the cœlom into two compartments, cardiac and abdominal, in the latter of which the lungs are situate. In birds appears the intermediate stage, where the greater part of the lung has become extruded from the abdominal cavity. In the third stage, which is reached in mammals, the lungs are now entirely extra-abdominal, being separated from the abdominal cavity by a portion of its parietes. Hence the lungs, like the testicles, may be regarded as organs "extruded as herniæ from the abdominal cavity because of certain physiological conditions that became of functional importance in the course of evolution" (9). The lungs then, gradually assuming a position more cephalad, pass through the inner of the three muscular strata of the hind-part of the body-wall by means of an opening corresponding to the pleuro-peritoneal aperture, at the same time, by reason of their extra-abdominal growth, depressing this inner stratum within the cœlom. Their development proceeds within new spaces thus formed between the middle and inner primary layers of the body-wall, the mammalian pleural cavities.

2. *Evidence Derived from Nerve-supply.*

In the primitive state the diaphragm was near the head, but, during development, has gradually become displaced backwards, so that the primitive nerve, which was short, proportionately has become elongated so as to keep pace with the retrogression of its muscle. Thus is explained the extraordinary distance between the origin from the spinal cord of the phrenic nerve and its distribution. Cavalié (10) recognises three phylogenetic stages in the nerve-supply of the diaphragm. In the first stage, found only in vertebrates below birds, the diaphragm is supplied only by one dorsal set of nerves, the intercostals. In the second, in birds, two sets are found, viz., the intercostal nerves to the costal diaphragm, and the sympathetic system with the dorsal ganglia to both diaphragms. In the last stage, in mammals, and particularly in man, a third source, the phrenic nerve (which becomes preponderant) is superadded.

3. *Evidence Derived from Embryology.*

By those best qualified to judge the development of the diaphragm has been accounted the most difficult of embryological problems, since a consecutive series of embryos is hard to find, and, during development, the diaphragm migrates from head to abdomen with consequent modification of adjacent structures during its passage. The position of the manubrium (Th. I.), and of the central tendon of the diaphragm (disc between Th. VIII. and Th. IX.), are evidences of the originally high position of the thorax (11). This developmental problem has been vigorously attacked by careful and systematic examination of serial sections and reconstruction models of embryos of different ages, the foundation of the study having been well and truly laid by the classical researches of His. Still earlier, von Baer (12) had recognised the downward progress of the diaphragm, and its innervation from the nerves of the neck. The first observer, however, to give a connected account of the process was His, who located the *Anlage* of the diaphragm in a mass of tissue lying with the heart among structures belonging to the head, and containing within it the veins to the heart as well as the *Anlage* of the liver. In the words of His (13): "die Rückwand der Parietalhöhle besteht aus einer Substanzplatte, welche in frontaler Richtung von einer Seite des Rumpfes zur andern sich erstreckt, und an der von hinten her die Darmwand, von vorn her der Herzvorhof anhaftet. Ich bezeichne diese Substanzplatte als primäres Zwerchfell oder als Septum transversum." This same structure already had been described under the name of "mesocardium laterale" by Kölliker (14), who appears not to have noticed their identity. This splanchno-pleural septum transversum constitutes the primitive diaphragm, the influences which bring about its appearance being (*a*) the expansion and growth of the heart, and (*b*) the formation of the cranial flexure carrying the splanchno-pleure tailwards beneath the vitelline veins. Its anterior margin is concave, supports the heart, and gives attachment to remains of mesocardium anterius and posterius. Further progress of heart and venous system and appearance of air-breathing apparatus tend to development of the pericardium and permanent diaphragm. One of the most important events is the formation of the ductus Cuvieri and their subsequent conversion into superior venæ cavæ, which, encroaching on the iter venosum, lying as it does between these and the alimentary canal, finally cause its disappearance (15). The duct of Cuvier lies in the body-wall of the mammalian embryo, and enters the dorsal part of the septum transversum. The position of the latter, looked at from the side in an embryo 3 mm. in length, is very oblique; later it becomes pushed down into a more transverse position.

On the lateral aspect of the lung in a human embryo lies a fold with free crescentic lower margin; attached above to the anterior end of the Wolffian body, below to the liver, behind to the posterior cœlomic wall, and in front by its fixed border to the dorsal part of the septum transversum. This fold is the "pleuro-peritoneal membrane" (16, 17, 18) familiar to embryologists, the hinder portion of which has been termed the "pillars of Uskow" (19). Lockwood (20) has called it the "dorsal diaphragm," and, in common with many others, including Mall (21) and Piper (22), has regarded it as the part of the diaphragm which is first formed. Broman (23), however, subsequently pointed out that this so-called dorsal diaphragm takes no part in the formation of the diaphragm proper, and Keith (24) has demonstrated the true nature of this fold by finding its homologue among the tailed amphibians, where, in the female, it serves as the mesentery of the oviduct, and thus is seen to belong, not to the circulatory or respiratory systems but to the genital system. Hence for the earliest appearance of the diaphragm we have elsewhere to seek.

In addition to the pleuro-peritoneal membrane, Uskow (19) described another structure in the formation of the pericardium and adult diaphragm. This he termed the "pleuro-pericardial membrane," which in reality represents the upper layer of cleavage of the dorsal part of the septum transversum.

Two distinct embryonic elements, dorsal and ventral, together constitute the mammalian septum transversum. The dorsal portion corresponds to fusion of the amphibian cervical aponeurosis with the dorsal wall of the pericardium; the ventral half represents the septum transversum of fishes and amphibia. It is worthy of note that the whole of the septum transversum of mammals is not homologous with the structure of the same name in fishes and amphibia, but only the ventral portion. Included in the dorsal mass is the duct of Cuvier, and into it in forward and outward directions extend the lung-buds, which by gradual process of growth cleave the dorsal mass into an upper or pleuro-pericardial layer and a lower or pleuro-peritoneal. This process represents the perforation and downward displacement of the amphibian diaphragm by the extrusion from the abdominal cavity of the lungs, and their growth and development between the inner and middle of the three primary layers of the parietes. The diaphragm develops beneath the fourth and fifth cervical segments, "processes from the muscle-plates of which enter the basis of the diaphragm, and form part at least of its muscular substance. The muscle-buds carry their nerve—the phrenic—with them. The descent of the heart, the retrogression of the stomach, and the development of the lungs lead to the diaphragm being pushed backwards until it assumes the adult position" ([25]).

In all probability the diaphragm originates by fusion of five elements—one mesial, two ventro-lateral, and two dorso-lateral. Of these the mesial and ventro-lateral are the chief, constituting as they do four-fifths of the total superficies, and together forming the septum transversum. The dorso-lateral elements enter into the composition of the remainder, and are relatively of less importance, being found in mammals only, as comparatively late structural additions. These dorso-lateral portions unite later with the septum transversum to form the primitive "pleuro-peritoneal septum," and thus to complete the partition of the cœlom into pleural and peritoneal cavities. The mesial (mesenteric) element is formed by junction of the ventral and dorsal portions of the mesentery of the fore-gut. The development of the ventro-lateral elements is not yet fully understood. They are said to appear very early (third week), while yet the vitelline veins terminate in the sinus venosus, and before the liver-bud has grown out. The vitelline veins pass obliquely in the ventral mesentery from the yolk-sac to the sinus venosus. They become dilated so as to produce their covering of splanchnopleure until lateral folds are formed, which come in contact with, and adhere to, the somato-pleure. In this way the mesentery (mesial part of the diaphragm) becomes adherent to the lateral somatic walls ([25]).

When the embryo reaches the length of 20 mm., the pleuroperitoneal apertures become obliterated chiefly by the cephalad growth of the liver within the dorsal mesentery. Since this growth takes place to a much less extent on the left side, the left pleuro-peritoneal communication remains patent more often than the right, hence the greater frequency of left diaphragmatic hernia. Other factors which probably share in the completion of the diaphragm are the projection of the Wolffian ridges, and the formation of the suprarenal body.

About the end of the second month muscle-fibre has already begun to appear in the neighbourhood of the lower end of the œsophagus; in the third month the diaphragm becomes more fully developed by the appearance of peripheral muscle-fibres, which spring from its costal portion.

4. *Evidence Derived from Comparative Morphology.*

Search for traces of a structure homologous with the mammalian diaphragm is necessarily confined to the vertebrate order, and it is amongst Anamnia that we find the first indication. In Pisces the cœlom is undivided by any septum, but when we come to amphibians, in Anura we find the first recognisable elements of the diaphragm in two muscular bands, dorsal and ventral, whose function is wholly circulatory. Turning next to Amniota, we find that most Reptilia have an undivided cœlom with no structure morphologically corresponding to the mammalian diaphragm. In Crocodilini, however, despite independent origin, there is strong functional homology, for a specialised subperitoneal muscular sheet springs from the pelvis, being derived from the same deep rectus sheet as the sterno-costal part of the mammalian diaphragm, and functionally homologous with it. Gegenbaur (26), through inability to reconcile the origin of this peritoneal musculature with its homology, did not regard it as a diaphragm. In the box-tortoise (*Emys Europæa*), Owen (27) has described a form of diaphragm which springs by three sheets "from the bodies of the 4th and 5th thoracic vertebræ, and from the rib of the 3rd thoracic: the two posterior unite to apply themselves to the mesial surface of the lung; the third sweeps over the outer surface, and is reflected from its lower border upon the peritoneum." Tortoises and turtles have also been examined by Weir Mitchell and Moorhouse (28), and by Keith (29), the latter regarding the diaphragm in these primitive reptiles as in type amphibian. In Aves indications of a muscular investment of the lungs are present, best seen in Apteryx (Gegenbaur). The lower surface of the lung is separated from the liver by a thin fibrous membrane or septum, called "the pulmonary aponeurosis," into which are inserted a variable number of muscular bands (costo-pulmonary muscles): these arise from the vertebral ribs, and are supplied by the intercostal nerves. "The avian diaphragm is the cervical aponeurosis of the amphibia, which, with the inner layer of muscles, has been separated from the middle (intercostal) and outer layers of the body-wall by the development of the lung. But the muscular element belongs, not to the cervical, but to the dorsal part of the transversalis sheet" (29). Among mammalia "the diaphragm is most muscular, longest, and most oblique in cetacea, in which the central tendon is almost obsolete: by rising so far back, it permits the proportional extension of the lungs, which in the dugong and the manatee act as air-bladders. In the perissodactyle ungulates, in which the movable ribs are numerous and continued nearly to the pelvis, the diaphragm is also extensive, and much arched towards the thorax" (29). The diaphragm, as such, is not more completely developed in man than in the monotreme (30). In the porpoise (*Phocæna communis*) there is no tendinous centre. Its pillars are slender and tendinous, and are attached to the ventral face of the vertebræ, as far back as the ninth lumbar. A strong fibrous aponeurosis is continued back over the sub-vertebral muscles to the pelvic bones. Between these bones and the ends of the transverse processes of the 28th and 29th vertebræ the aponeurosis forms almost a distinct fibrous band. In the hedgehog ossification occurs on each side of the aortic opening (31).

Whether with Balfour and Semper we should regard man as derived from primitive annelid; or, with Gaskell, from protostracan arthropod; or, with Huxley and with Keith, from tailed amphibian, is a matter which admits of large argument based on inconclusive evidence. Taking the relationships of the diaphragm as the main point at issue, the last view is the one which has most in its favour. In the elucidation of this problem the work of Keith (32) is of such far-reaching interest and importance that I will endeavour briefly to summarise the method and results of his inquiry. Starting with "the intimate structural and functional relationships which exist between the central tendon, the pericardium, and roots of the lungs," he inferred from the approximately vertical position of the crura and the insertion of these and of the sterno-costal fibres on opposite sides of the central tendon, that, on inspiration, the central tendon, pericardium, heart, and roots of lungs must of necessity move downwards and forwards. X-ray investigation has confirmed this. The close relationship of the diaphragm with the pulmonary roots suggested an idea, found later to be only partially true, that the diaphragm appeared first, not as a partition, but as muscular bands which acted directly on the roots of the lungs, pulling them during inspiration downwards and forwards. Investigation in infants shows that the diaphragm must originate within the layers of mesentery which separate the right from the left half of the cœlom, since the diaphragm lies between the pleuro-peritoneal openings. Probably in the ancestry of the mammalia the whole insertion of the dorsal part of the amphibian diaphragm was transferred to the mesentery of the fore-gut, and, within that structure, reached the pericardium, not on the lateral aspect of the lungs, but on their mesial aspect. Evidence derived from the nerve-supply predicates two distinct muscular elements in the diaphragm. "It is impossible to conceive that the mammalian diaphragm arose from any structure found in extant birds or reptiles," and, on reviewing the latter-day amphibia, homologues were discovered amongst Anura which functionally correspond with the mammalian diaphragm in regard to its primary and most important faculty of filling the heart with blood. As exemplified by its primitive arrangement in fishes, the septum transversum is correlated in function with the amphibian diaphragm for the same circulatory object, serving, as it does, to separate two cavities in which the conditions of circulation are at variance. Further developmental evidence shows that the origin of the mammalian diaphragm must be sought in that of the tailed amphibia, until finally one reaches the conclusion that the mammalian diaphragm represents the cervical wall or diaphragm of the amphibian abdominal cavity which is perforated and displaced by the development of the lungs, the point of perforation becoming the pleuro-peritoneal aperture.

In 1895, in a paper on the anatomy of the Surinam toad (*Pipa Americana*), F. E. Beddard (33) directed attention to a narrow muscular sheet, which, arising close to the rectus femoris, expands fan-wise as it proceeds forwards, and gains insertion into the dorsal aspect of the œsophagus, root of lung, and a fibrous expansion which, investing the liver and continuous with the pericardium, constitutes the cervical aponeurosis of the abdominal cavity. This structure Beddard regarded as homologous with the mammalian diaphragm, and compared it with the rudimentary diaphragm of Rana, which he considered to represent the anterior portion of obliquus internus. A special muscle running from ilium to lung and œsophagus corresponding with that found in Pipa was found, too, in the

African toad (*Xenopus*) (³⁴). This dorsal muscular sheet probably represents only the spinal segment of the diaphragm, as has been shown by Keith (³²), who has minutely reinvestigated the anatomy of these toads, and has pointed out that the amphibian diaphragm is composed of three parts—a spinal portion derived from the anterior or cervical part of the transversalis sheet, a ventral part from the fourth segment of the rectus sheet, and a central part from the cervical amphibian aponeurosis referred to above.

These tail-less forms (*Xenopus*, *Pipa*) "have certainly been derived from long-tailed amphibians, and, on the supposition that the mammalia have also been evolved from a primitive amphibian form (stego-cephalia), it is probable that the same elements which gave rise to the diaphragm in Anura may also have become modified to form a corresponding structure in mammals (³²).

B.—MORPHOLOGICAL MUSCULAR RELATIONSHIPS.

The primary system of musculature, of which the structure of the leech is an example, consists of a single muscular plane from endoderm to ectoderm. The most complicated muscular arrangements gradually have been evolved from this simple type merely by successive segmentations which change the direction of the muscle-fibres. As the late Professor G. M. Humphry (³⁵) pointed out, the imperfect segmentation and individualisation of the muscles of Urodela to some degree affords a natural method of determining the relations which the muscles of the higher animals bear to one another and of grouping them, the segmentation into planes being merely the result of the variation in direction of fibres at different depths. The salient morphological relationships of the diaphragm I have tried to indicate in the accompanying Table I., where we see the trunk-musculature separated by the intervention of the primitive vertebral axis into two main dorsal and ventral groups which are homologous with similar dorso- and ventro-lateral groups of the broad lateral muscle of fishes and tailed amphibians. Those of the dorsal group become spinal muscles; the ventral set are still further subdivided into ventro-mesial and ventro-lateral divisions. In all but the lowest vertebrates, whilst the mesial group of ventral muscles retains the longitudinal direction of its fibres, and is the least altered, the lateral portion of the ventral muscular sheet is divided into three chief planes. In the ventro-mesial set the rectus layer, although lost over the thorax, is prolonged into the neck as the anterior flat muscular layer attached to hyoid bone, thyroid cartilage, and mandible, and becomes apparent in the abdomen as the rectus and pyramidalis, possibly, too, as the longitudinal fibres of the quadratus lumborum. The functional relationship of this latter with the scaleni is seen in their opposite pull at each end of the thorax. The abdominal layer of the rectus sheet, of which pyramidalis forms part, has undergone least change in position and direction of its fibres.

TABLE I.

Muscles of the Trunk.		deep layer	middle layer	superficial layer
dorsal spinal muscles				
ventral (including the muscles variously termed hypaxial, hyposkeletal, or subvertebral)	ventro-mesial	sterno-thyroid sterno-hyoid omo-hyoid genio-hyoid genio-glossus diaphragm, sterno-costal part	first three segments of cervical part of rectus sheet	muscles of face, ear, and scalp scaleni
		rectus	deep layer of fourth segment	platysma
		pyramidalis quadratus, longitudinal fibres	abdominal part of rectus sheet	intercostals, internal and external levator costarum
	ventro-lateral	longus colli rectus capitis anticus major diaphragm, dorsal part subcostals	cervical part of transversalis sheet	obliques, internal and external
		triangularis sterni	thoracic part of transversalis sheet	rest of quadratus
		transversalis	abdominal part of transversalis sheet	
		levator ani	pelvic part of transversalis sheet	
		sacro-coccygeus anticus		

From the cervical part of the transversalis sheet is formed the diaphragm.
From the thoracic part of the transversalis sheet is formed the triangularis sterni.
From the abdominal part of the transversalis sheet is formed the transversalis abdominis.
From the pelvic part of the transversalis sheet is formed the levator ani.

Thus we see that one great muscle-plane, compressor in function, becomes divided into a series of separate muscles each with still more specialised functions. Just as the triangularis sterni constricts the anterior part of the thorax, so the transversalis compresses the anterior part of the abdomen, the crura of the diaphragm compress the liver and stomach, and the levator ani the pelvic viscera. The triangularis sterni is the direct cephalad continuation of the transversalis abdominis, and with its substance are frequently blended fibres of the diaphragm.

In like manner as the diaphragm above has important relations with the alimentary canal (œsophageal portion), so the pelvic diaphragm or levator ani below has similar relations with the alimentary canal (rectal portion). In the splitting up of muscles into planes, the fibres of those portions which go to form the diaphragm undergo change in direction.

C.—DETAILED DESCRIPTIVE ANATOMY.

"*In a practical point of view anatomy is of no use unless it can be realised on the living body*" (Sibson).

The diaphragm consists of transversely striated (voluntary) muscle with a fibrous-tissue centre, and may be divided into the following portions:—

I. *Dorsal Portion.*—Vertebral or spinal division (pars spinalis vel lumbalis), consisting of: (*a*) crural fibres; (*b*) arcuate fibres.

II. *Ventro-lateral Portion.*—Sterno-costal division (pars sterno-costalis), consisting of: (*a*) sternal fibres; (*b*) costal fibres.

III. *Intermediate Portion.*—Central division or tendon (centrum tendineum vel phrenicum); cordiform or trefoil tendon.

Of these divisions I. and II. are mainly muscular, whilst III. is almost entirely tendinous.

I. *The vertebral or spinal division* has a strong fixed origin by means of *a*, crural, and *b*, arcuate fibres from the lumbar vertebræ and arcuate ligaments.

(*a*) *Crural Fibres.*—The pillars of the spinal portion, intimately blended at their origin with the anterior common ligament of the vertebræ, arise, each in slightly different manner, from the antero-lateral aspect of the lumbar vertebræ. *The right crus*, the longer, larger, and stronger of the two, arises as a massive pillar, wholly tendinous for its initial eight centimetres or thereabouts, from the first three or four lumbar vertebra and corresponding discs. Most frequently it springs from the upper portion of the right half of the anterior surface of the fourth lumbar vertebra by a flattened tendinous origin, being intimately blended with its fellow of the opposite side and with the anterior common ligament, with which it is directly continuous. From this attachment, passing vertically upwards over the intercentral disc between the third and fourth lumbar vertebræ and the bodies of the third and second lumbar vertebræ, to which it also gains strengthening attachment, the tendon becomes narrower at the expense of its internal border, and at the same time thicker, so that opposite the middle of the second lumbar vertebra in cross-section it is oval. By the time that it reaches the middle of the body of the first lumbar vertebra, it has become almost circular, and at this level the pillar begins to broaden and thicken, the lateral expansion being more marked at the inner margin. Its posterior surface gives gradual origin to muscle-fibres which spring from a line passing obliquely from a point on its external surface, in an adult about 8 cm. above its point of origin, upwards and towards the middle line. The tendon at its inner margin is continued over the front of the aorta in the form of an inverted U to meet its fellow of the opposite side. Thus a thin narrow tendinous arch, sometimes termed "the middle arcuate ligament," is formed, from the edge of which a closely set fringe of muscular fibres ascends. This straightway divides into two layers, the anterior and larger layer passing either vertically or obliquely towards the right and bounding the right side of the œsophagus, the posterior and smaller layer going to the left and bounding the left side of the œsophagus, both sets of fibres reuniting anteriorly to gain insertion into the posterior angle of the trefoil tendon. The greater part of this posterior layer usually lies superficial to, or, in some cases, alongside of, the mesial border of the left crus.

To the outer side of the right crus and parallel with it arises an additional pillar, the *right accessory crus* (crus accessorius). At times this is continuous with the right crus at its origin for a distance of a few millimetres, or may spring mainly from the body of the second lumbar vertebra and the disc between the second and first, and then, becoming separate from the right crus, passes vertically upwards as a thin slip of variable size, sometimes absent altogether, occasionally found on the inner side of the main crus, and about one-third its size, entirely tendinous for the lower third of its extent, and muscular for the upper two-thirds. Through the narrow vertical interval between the right bundle and its accessory crus pass the great and lesser splanchnic nerves.

The left crus blends with the right crus and with the anterior common ligament of the vertebræ. It is smaller and shorter than the right crus; most often it springs from the antero-lateral aspect of the bodies of the first and second, sometimes the third lumbar vertebræ, lying more on the side of the spine than the right crus, and occupying a plane posterior to it. To some extent it is overlapped by the abdominal portion of the aorta. In like manner to its fellow of the opposite side first it narrows as it ascends, its anterior surface similarly giving rise to muscle-fibres, the inner ones vertical or passing alongside of the right crural fibres to the right of the œsophagus, the outer ones proceeding obliquely outwards to their insertion into the central tendon. A few weak fibres sometimes proceed from the mesial aspect of the left crus, and, passing upwards obliquely towards the right, lose themselves by blending with those of the right crus. These fibres, however, take no share in the formation of the œsophageal opening. The inner margin of the left crus remains tendinous, and meets the corresponding portion of the right crus in the manner above described, to form a tendinous arcade, the summit and mid-point of which is placed a little to the left of the middle line of the vertebral column, forming the anterior margin of the aortic arch. From the anterior surface of the first and second lumbar vertebræ and intervening disc fine tendinous fibres are sent. On the posterior surface of the aorta these appear flattened out, then, curving so as to encircle it (in a manner resembling that in which the tendon of flexor sublimis in the hand splits to enclose flexor profundus), they unite with its coat, and finally join the deep surface of the tendinous arcade.

In the ordinary adult male the interval between the pillars of the diaphragm at its widest part measures about 20 to 25 mm., and from origin of chief crural fibres to summit of aortic ring about 80 mm. From origin to insertion the right crus measures about 15 cm., and the left crus about 14 cm. The fleshy fibres of the right crus pass usually, but not always, superficial to those of the left crus, and then encircle the gullet, forming an elliptical opening for its passage, and both sets of fibres are attached to the central tendon along the inner three-quarters of the posterior Λ-shaped indent.

Three crura are described by the German school of anatomists, the first two on each side corresponding to the crura above mentioned, whilst a third, or supplementary crus laterale, is said to take origin from the lateral surface of the first or second lumbar vertebral body, and from a strip of fascia which extends thence in front of the psoas to the transverse process of the first lumbar vertebra. There is often no sharp division between this crus laterale and the crus proper. Hence it is better to consider the former in its proper connection as a bundle of arcuate fibres, since it is much shorter and weaker than the true crura, and in function different from these.

By the American school the external and internal arcuate ligaments are described as constituting a lateral crus, an intermediate one being stated to arise from the second and third lumbar vertebræ, whilst the medial crus arises from the bodies of the third and fourth. The action of the so-called "lateral crus" much more closely resembles that of the sterno-costal portion than the crura proper.

(*b*) *Arcuate Fibres.*—The *medial lumbo-costal arch* (ligamentum arcuatum internum) is a thickening of that portion of the iliac fascia which covers the psoas muscle. At its inner extremity this fascial band is attached to the lateral surface of the second (or first) lumbar vertebra; beneath it on each side passes the ganglionated cord of the sympathetic. The fibres take a forward, upward, and outward course to their insertion along the outer quarter of the posterior Λ-shaped indent of the central tendon.

The *lateral lumbo-costal arch* (ligamentum arcuatum externum), weaker than the internal, is formed by a thickening of the upper border of the fascial investment of the quadratus, *i.e.* the anterior layer of the lumbar fascia. At its inner end it springs from the transverse process of the second or first lumbar vertebra; at its outer end by an inconstant attachment it is affixed to the last rib. The muscle-fibres springing from this arciform band proceed upwards and outwards to gain insertion into the rounded posterior extremity of the corresponding lobe of the central tendon external to the above-mentioned fibres from the internal arcuate ligament. Both sets of fibres are more oblique in direction than is usually represented.

The *sternal portion* arises by two short narrow slips, usually muscular, sometimes aponeurotic, from the lower border and posterior surface of the ensiform cartilage. These slips, diverging slightly, proceed obliquely upwards and backwards to gain insertion into the anterior margin of the central tendon. Not infrequently they are absent.

II. *The Sterno-Costal Division.*—The *costal portion* takes origin from the circumference of the thorax by means of five flattened muscular fascicles which arise from the lower borders and inner surfaces of the cartilages of the seventh to the eleventh ribs, rarely from the twelfth, and in well-developed muscular subjects also from the adjacent bony surfaces. The lower margin of this costal portion in outline is serrate, one or more dentations being attached to each rib, interdigitating with like fibres of origin of the transversalis abdominis.

The anterior fibres of this portion are the shortest and proceed in a direction upwards, backwards, and towards the middle line. As the muscle is traced backwards its fibres are seen to elongate, the intermediate ones passing upwards and backwards with varying degrees of obliquity for the lower two-thirds of their course, and then sweeping inwards towards the middle line. The fibres which spring from the cartilages of the eighth and ninth ribs are the longest. The posterior fibres pass upwards and towards the middle line, the innermost ones being frequently directed upwards and inwards, crossing those springing from the external arcuate ligament, which pass upwards and in varying degree outwards. As a result of this crossing a triangular interval is left.

This peripheral muscular layer gains its insertion by becoming continuous with the margin of the central tendinous layer around the thoracic circumference, except posteriorly, where it gives place to fibres from the external arcuate ligament, and anteriorly, where it joins the sternal fibres. At each of these two spots, however, the ring is completed only by means of the upper portion of the costal fibres, two triangular lacunæ being left: (1) costo-sternal; (2) costo-arcuate, the nature of which has been explained already in the section on Morphology.

Lacunæ—(1) *Costo-sternal.*—Between the sternal and costal portions is a small triangular interval, with apex where costal and sternal fibres join for insertion into the central tendon, through which interval the loose areolar tissue of the thoracic cavity is continuous with the subperitoneal cellular tissue of the abdominal cavity. Owing to this direct communication it is easy for processes of inflammation, at times proceeding to suppuration, to spread by continuity from one great serous cavity to the other. This interval serves for the transmission of the superior epigastric branch of the internal mammary artery, with its corresponding vein, and of some lymphatics passing to the inferior sternal lymph-glands from the convex surface of the liver and the abdominal wall.

(2) *Costo-arcuate.*—Between the muscular fibres which arise from the eleventh rib, or occasionally from the twelfth, and those which spring from the external arcuate ligament, in about 60 per cent. of cases is seen a triangular interval of greater or less extent. Here again a pad of lax areolar tissue is the only means of separation of pleura from peritoneum.

III. *The Central Division or Tendon.*—This strong, thin, glistening aponeurosis, in function serving to support the heart, and intimately fused with the pericardium and contractile elements of the muscle of which it forms the mid-portion, consists almost entirely of a dense unyielding feltwork of fibrous tissue.

Although the disposition of the strands composing this feltwork varies with the individual, there is, nevertheless, a broad general arrangement. The chief bundles are two in number. The anterior is U-shaped, and springs by expanded fan-like extremities continuous with the right sterno-costal and costal muscular fibres (Fig. 1, *a*). The bundle becomes narrower and condensed at its middle (*b*), which forms the posterior boundary of the opening for the inferior vena cava. In like manner the posterior fascicle springs fan-wise from the posterior blunt extremities of the alæ (Fig. 1, *c*), and, sweeping forwards in a semicircle, becomes condensed in its mid-portion, and forms the anterior boundary of the caval aperture. Usually it lies above the first-mentioned bundle, but the limbs may interlace or overlap. Other less-defined strands pass in all directions, the pericardial portion being the most closely woven.

The tendon consists of three portions, two wings and a centre. The right ala forms the largest part, and extends farther backwards than the left, which is the smallest. The centre is intermediate in size and relatively ventral in position, two-thirds of its transverse diameter being situated to the left of the middle line, and more or less fused with the left wing. Between the centre and right wing is the caval opening. The central tendon has a shape peculiarly its own, which has variously been stated to resemble a trefoil, horseshoe, or kidney (*vide* Fig. 1). Its anterior margin is convex, its posterior margin forms a triangular hollow for implantation of the crura.

Openings in the Diaphragm.

There are three main openings in the diaphragm and several smaller ones. The main apertures transmit the aorta, œsophagus, and vena cava inferior.

The *aortic opening* (hiatus aorticus) lies at the lowest level opposite the twelfth thoracic vertebra, slightly to the left of the middle line, and in front of the vertebral column. It is placed behind the diaphragm, and its size and position undergo no change when the diaphragm contracts. It consists of an oval osseo-aponeurotic aperture, formed anteriorly by the ligamentum arcuatum medium, which joins the crura: posteriorly it is bounded by the anterior common ligament. It transmits the aorta, frequently the vena azygos major, and between these the thoracic duct, together with the left sympathetic nerve occasionally. Sometimes tendinous fibres are prolonged across the bodies of the vertebræ from the inner aspect of the crura, which pass behind the aorta and thus convert this opening into a fibrous ring.

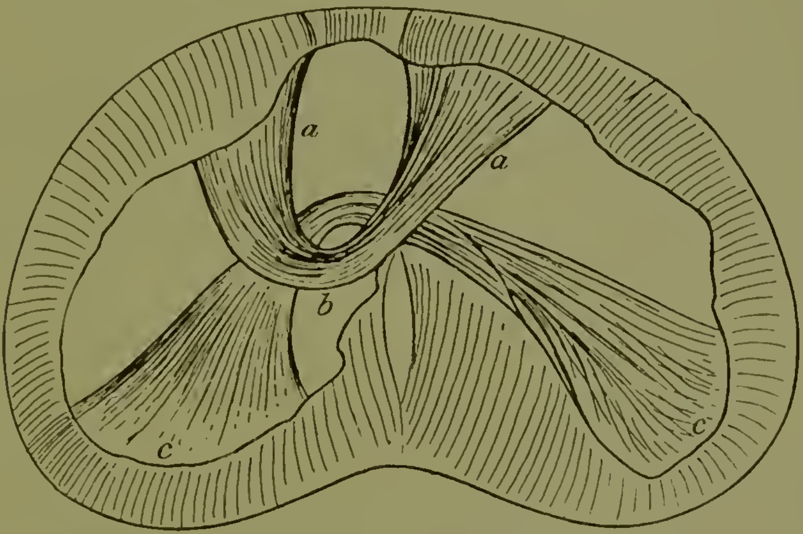

Fig. 1 (diagrammatic).

The œsophageal opening is placed at the level of the body of the tenth thoracic vertebra, and transmits (*a*) the œsophagus, (*b*) the two vagi—the right in front of the œsophagus, the left behind,—(*c*) descending branches (œsophageal) of the thoracic aorta which anastomose with œsophageal branches of the coronary. It lies just to the left of the median line of the body, on a plane anterior to that of the aortic opening (owing to the forward curving of the crura), its shape being elliptical, with the long axis directed upwards and forwards. It is situate in the muscular part of the diaphragm which is thickest and strongest, the margins of the ellipse being formed by encircling mesial fibres of the right crus.

The left crus, as we have seen above, is not concerned with the formation of the œsophageal aperture, the margins of this opening being entirely formed by the fibres of the right crus. This statement is in accord with the recently published observations of Low (36), who further describes the muscle of Treitz (suspensory of duodenum) as springing from the right crus as it lies against the right margin of the œsophagus. At times the anterior extremity of the opening is formed by the posterior edge of the central tendon. A loose feltwork of areolar tissue attaches the structures which traverse the aperture to its margin.

The caval opening (foramen quadratum) is placed at the junction of the right with the middle leaflet, opposite the disc between the eighth and ninth thoracic vertebræ. In shape it is roughly quadrilateral, and is bounded by tendinous fibres which decussate round its margin, and are themselves attached to the wall of the inferior vena cava which it transmits. The right crural pillar is pierced by the right greater and lesser splanchnic nerves, sometimes by the vena azygos major; the left by the left greater and lesser splanchnics and the vena azygos minor.

In a series of twelve male and female adults I found the average superficial area of the diaphragm, measured on its under surface, to be 942 sq. cms.: the lowest reading was 836 sq. cms., and the highest, 1027 sq. cms. The average weight of the diaphragm is 330 grams, and of the crura 63 grams, so that the weight of the crura is about one-fifth of the total weight, and may vary between one-fourth and one-sixth. In both heart and diaphragm there is 1 sq. mm. of arterial cross-section for every 10 cc. of muscle (the biceps has 1 mm. for each 16, and tibialis anticus 1 mm. for each 18) ([37]).

D.—THE NERVE SUPPLY OF THE DIAPHRAGM.

Being polymeric, the diaphragm is necessarily heteroneural, and receives its innervation from the phrenic (motor), and from motor branches from the seventh to the twelfth intercosal nerves, which also contribute to the sensory supply of the periphery of the muscle. Fibres for the supply of the blood-vessels are furnished by the sympathetic system.

A. *The phrenic nerve* (internal respiratory nerve of Bell) extends from the cervical plexus of the spinal cord to the diaphragm. It is noteworthy alike for the importance of its functions, as well as for the length of its course, which is due to the distance of its distribution from its spinal origin.

(*a*) *Origin.*—The phrenic nerve takes origin as a deep internal muscular branch of the cervical plexus, and, springing mainly from the fourth cervical nerve, is, in the majority of cases, reinforced by additional roots from the third (either directly, or through the nerve to the sterno-hyoid), and fifth (either directly, or through the nerve to the subclavius muscle) ([38]). Additional origin has been recorded in a negro from the fifth cervical ([39]).

(*b*) *Course.*—After the nerve-trunk has been formed by junction of its roots at the level of the second cervical vertebra, about 25 mm.

above the carotid tubercle, it descends almost vertically with a slight inclination inwards upon the anterior surface of the scalenus anticus muscle. At the lower border of this muscle it enters the superior aperture of the thorax, and makes a slight curve on the inner aspect of the apex of the lung. Then, traversing in order the superior and middle mediastina, it passes downwards in front of the root of the lung, and, running along the lateral aspect of the pericardium, reaches the diaphragm, where it ends. The nerve is accompanied through the thorax by the superior phrenic artery (comes nervi phrenici), which is a long slender branch from the internal mammary, and corresponding vein.

(*c*) *Relations.*—i. *In the Neck.*—Firstly the nerve is attached by a layer of cervical fascia to the anterior surface of scalenus anticus. It lies deep to the posterior belly of the omo-hyoid muscle, which crosses it obliquely in forward and upward direction, and, at the root of the neck, receives a branch from the middle or lower cervical ganglion of the sympathetic. From this point onward, until its termination, the phrenic on each side has different relationship with adjacent structures. Here, too, the right phrenic nerve crosses the second part of the subclavian artery, whilst the left phrenic crosses the first part: on each side the nerve is posterior to the subclavian vein.

ii. *In the Superior Mediastinum.*—The right phrenic lies on the outer side of the right innominate vein and superior vena cava, and does not come into relationship with the right vagus. The left phrenic passes between the left subclavian and carotid arteries, and crosses in front of the left vagus and left side of the aortic arch.

iii. *In the Middle Mediastinum.*—On the right side the phrenic nerve descends almost vertically between pericardium and pleura, lying in relationship with the right auricle below the level of the root of the lung, which it crosses anteriorly, and having the mediastinal pleura to its outer side. On the left side, in order to reach the diaphragm, the nerve has to follow a much longer course. The reasons are as follow: (*a*) That the heart, together with its pericardium, extends considerably further to the left of the middle line than to the right, consequently the left phrenic nerve cannot descend vertically like the right, but is obliged to curve outwards and to the left in order to get round the apex of the heart; (*b*) that the vault of the diaphragm does not rise as high on the left as on the right, and the convexity of its curve is not as great.

(*d*) *Branches.*—The main trunk of the right phrenic ends by piercing the diaphragm on the outer side of the caval orifice, the left ends about 3 cm. external to the tendinous centre. Hilton (40) has shown that the main distribution of both nerves upon the under surface of the diaphragm obtains in order that "these threads upon which our lives hang" may be protected from injurious pressure during respiration. The phrenic nerves divide into superior and inferior branches for the supply of the muscle. The superior branches run for some distance between the pleura and diaphragm, and finally are distributed to the thoracic surface of the muscle which they enter. The inferior branches, piercing the muscle, ramify between diaphragm and peritoneum for some distance. They give small filaments to the peritoneum, and then penetrate the diaphragm from below. "The pleural and pericardiac branches are given off during the passage through the middle mediastinum. The branches to the inferior vena cava, suprarenal capsule, and liver arise after communication of the phrenic nerve with the diaphragmatic plexus of the sympathetic on the abdominal surface of the diaphragm" (41).

In order, therefore, the branches are:—

1. Muscular to diaphragm
    - *a.* subpleural;
    - *b.* subperitoneal.
2. Pleural.
3. Pericardiac.
4. Peritoneal
    - *a.* to peritoneum, lining abdominal wall from sternum to umbilicus;
    - *b.* to coronary, triangular, and suspensory ligaments of liver.
5. Caval.
6. Right auricular (Luschka).
7. Capsular (Cunningham).
8. Hepatic.

(*e*) *Variations.*—The phrenic nerve may pierce the scalenus anticus muscle, at the same time giving to it a small branch. It may pass either in front of the subclavian vein (Quain), or through it (Longet). The nerve may be reinforced by additional twigs from the second cervical nerve, the sixth cervical nerve, the brachial plexus, the superior cervical ganglion, or the vagus. Occasionally an accessory nerve springs from the fifth and sixth cervical nerves, and, running downwards with the phrenic, joins it after a lengthy course within the thorax.

(*f*) *Communications.*—α. *With the nerve to the subclavius* at the root of the neck by a fine filament which links together the two parallel nerves in front of the attachment of the anterior scalene muscle.

β. *With the cervical portion of the sympathetic* by two branches; one, more or less transversely disposed, connects the two nerves in the deep layers of the neck; a second, situated below the preceding, turns forward and joins the phrenic in front of the subclavian artery (42).

γ. *With the ansa hypoglossi* (Hirschfeld, Valentin, Wrisberg, Testut), or its branch to the sterno-hyoid (Cunningham), by a slender thread. This communication is not infrequently absent.

δ. *With the seventh to the eleventh intercostal nerves.*

ε. *With the solar plexus*, by means of the sympathetic system, which forms a delicate network of pale fibres which penetrate the muscle-fibres of the diaphragm along with the superior and inferior phrenic arteries, this being termed the *diaphragmatic plexus*. In this plexus small ganglia may be found.

At the point where the phrenic nerve joins the plexus on the right side a ganglion is formed (Schwalbe), which is made up of fibres from the solar plexus and cœliac ganglion, and is called the *diaphragmatic ganglion;* from this filaments proceed to the hepatic plexus, inferior vena cava, and suprarenal body.

ζ. *With the accessory nerve when present* (Blandin, Valentin).

η. *With the vagus rarely* by an extremely slender filament (Sappey).

B. *The Seventh, Eighth, Ninth, Tenth, and Eleventh Intercostal Nerves.*—These nerves pierce the attachments of the transversalis abdominis and diaphragm at the anterior ends of the corresponding intercostal spaces, and supply the costal portion of the diaphragm at its periphery. The terminal branches of the phrenic together with branches from the ninth, tenth, and eleventh intercostal nerves form a plexus within the muscular substance of the diaphragm (43).

E.—THE LYMPHATIC SUPPLY OF THE DIAPHRAGM.

Both the superior and inferior surfaces of the diaphragm are richly supplied with lymphatic trunks which accompany the blood-vessels. In the more lax connective-tissue they form fairly straight, cylindrical, anastomosing channels; but, where subjected to compression by the dense fibres of the central aponeurosis, they become merely tortuous and flattened chinks.

I do not propose in detail to describe their distribution, for this is fully dealt with in the various excellent works on the general anatomy of the absorbent vessels. The main divisions which concern us here are, (*a*) those draining the upper and lower surfaces of the diaphragm, and (*b*) those which drain the peritoneal cavity and pierce the diaphragm. In the dissemination of pathological processes the perforating lymphatics in all probability take large share, since they constitute a direct link between thoracic and abdominal cavities. In animals the existence of these lymph paths has long been recognised; but it is only of late, through the work of Kuettner (44) and others, that we have learnt that, whilst each half of the diaphragm possesses its own lymph-territory, which communicates with adjacent tracts by means of lymph glands only, the muscle as a whole has anastomotic communication with pleura, pericardium, and peritoneum. Exactly how the process takes place is not yet fully understood. Stomata in the diaphragm were described by von Recklinghausen (45) in 1862, and, until recently, his views have met with general acceptance. Some authors, however, deny that these openings exist, amongst them Sabin (46), who regards the lymph paths as a separate system of modified veins which have no connection with the connective-tissue spaces or large serous cavities. Notwithstanding that the openings "are far from representing permanently open channels of communication between the serous cavities and the vessels" (47), in places, probably, nothing is interposed beyond the endothelium of the lymphatic on the one side, and the endothelium of the serous cavity on the other. Muscatello (48) believes that leucocytes, after ingesting particles, force their way through the membrane, being immediately followed by a rush of free particles, which continues until the space again closes. Muscatello's opinions are confirmed by the experiments of MacCallum (49) with particles of carmine and Indian ink. This observer describes two endothelial layers with very thin basement membrane between, the lymphatics at these points being dilated into lacunæ. He assigns the chief rôle in the transmission of particles to the phagocytes—chiefly polynuclear leucocytes—and a lesser part to the pumping action of the diaphragm, which is said to force particles between the lining cells from the peritoneal cavity to the lymphatic lacunæ. The experiments of Buxton and Torrey (50) show that absorption from the peritoneal cavity takes place mainly by the anterior mediastinal route, most if not all of the conveyed particles lodging in the anterior mediastinal lymph nodes, of which the most prominent and constant are an upper pair (often three) situated in the first intercostal space. Other lower, less important pairs often are found in the third or fourth intercostal spaces. These nodes act as filters for the diaphragmatic lymph vessels which drain the peritoneal cavity. "Large bacilli, such as anthrax, can be absorbed through the diaphragm of a guinea-pig and reach the anterior mediastinal nodes in fifteen minutes or less" (50). Staphylococci and typhoid bacilli can also readily be absorbed through the diaphragm. The lymphatics of the crura drain into the lumbar glands.

F.—THE MEANS OF SUPPORT OF THE DIAPHRAGM.

These may be divided into superior or thoracic, and inferior or abdominal:—

A. *Superior or Thoracic Supports of the Diaphragm.*—The pericardium, as the name denotes, is the sac which surrounds the heart. Yet this office of investment is but one of the two distinct functions respectively corresponding to its two component layers. By its internal serous layer it is reflected upon the heart, and, diminishing friction by means of its apposed smooth and lubricated visceral and parietal portions, facilitates the action of that organ. The other function, with which we are now more directly concerned, depends upon the integrity of its strong dense inelastic outer layer, which, in structure, consists of several laminæ of mainly longitudinal white and yellow fibres. The base of this layer is firmly united to the upper surface of the diaphragm, inseparably to the middle leaflet of the central tendon at the circumference of the caval aperture, and, in lesser part, to the adjacent muscular surface especially on the left side, receiving around its periphery a continuous strengthening layer. Near the median line the connection is very firm, the fibrous structures of diaphragm and pericardium being continuous; elsewhere the attachment is more lax, and is effected chiefly by areolar tissue (51). Hence, as pointed out by Hilton,(52) in his classical work on Rest and Pain, the fibrous pericardium may be regarded as the fascial insertion of the muscular diaphragm. This stout fascial aponeurosis or outer layer, proceeding upwards over the heart, is prolonged into the sheaths of the great blood-vessels which ascend from the pericardial apex into the superior mediastinum. Thus it becomes blended with the adventitia of the two pulmonary veins and pulmonary artery on each side, and with the superior vena cava, aorta, and obliterated ductus venosus above. From this point it is continued upwards until it meets the innominate vein, to infold which it divides into two, one lamella passing behind the vein, while the other goes in front, at the same time gaining attachment to the interclavicular ligament and posterior border of the presternal notch. Above this level it constitutes the middle layer of the deep cervical fascia which covers the trachea and expands on each side to become continuous with the carotid sheath, and over the posterior aspect of the sterno-hyoid and sterno-thyroid muscles to be attached to the thyroid cartilage and body of the hyoid bone. At a short distance below the level of the hyoid bone this layer is joined by a weaker and more superficial one which springs from the anterior border of the presternal notch. These two layers enclose between them the small triangular suprasternal space. Laterally this middle layer passes upwards to insheathe the subclavius muscle, and to be attached to the posterior aspect of the clavicle, the first rib, and coracoid process of scapula. At this level also it forms a sheath for the subclavian vein, which thus is firmly bound to these structures. Thence proceeding vertically upwards, it divided to inclose the omohyoid muscle, and, again uniting, is attached to the hyoid bone. Above the hyoid bone this layer is thin and fibrous, below, it is strong, fibro-muscular, and inelastic. Thus, by reason of its mediate position between the respiratory muscles attached to the cervical fascia above and pulling upwards, and the diaphragm fixed to its base below and pulling downwards, the pericardium is kept tightly drawn.

So far we have dwelt with what justly may be termed the chief "superior ligament" of the diaphgram. This is not, however, the only means of support. Stability is afforded by additional anterior, lateral, and posterior attachments.

(*a*) *Anterior.*—Two weak and variable fibrous-tissue bands—the superior and inferior sterno-pericardial ligaments of Luschka—join the pericardium with the sternum. The superior of these, strong and sometimes cord-like (Macalister), running upwards and forwards, attaches the upper part of the anterior surface of the pericardium to the posterior surface of the presternum, whilst the inferior and weaker band, often double, proceeding downwards links the lower part of the anterior surface of the pericardium to the posterior surface of the metasternum.

(*b*) *Lateral.*—The prevertebral layer of the cervical fascia, entering the thorax, blends medially with the anterior common ligament of the vertebræ, whilst laterally it gives rise to strong and scattered fibrous bands, which descend through the superior mediastinum, on the right side along the œsophagus, on the left across the aorta, pass in front of the roots of the lungs, and are continued on the side of the pericardium as the ligamenta suspensoria of the diaphragm ([53]).

Another most important factor in holding up the diaphragm and in maintaining its curves, is the negative tension induced by the upward suction-action of the lungs. While the central part of the diaphragm is kept in position by the upward pull of its inelastic superior ligament, the lateral portions, which constitute the domes, are approximated to the corresponding basal concavities of the lungs. Thus, if the lungs undergo downward displacement, the position of the domes will, in like manner, be changed; if upwards, the domes will ascend.

(*c*) *Posterior.*—As we trace the right crus upwards we shall see that it is attached to the hinder part of the central tendon at its junction with the pericardium. At this level the inferior vena cava enters the heart, and the lateral or right fornix of the caval orifice is firmly fixed to the central tendon, and, indirectly through this medium, to the right crus, whilst its mesial or left fornix is free. The posterior wall of the pericardium serves as the band which joins the right fornix of the inferior vena cava to the lateral or right fornix of the superior vena cava, which, together with the right border of the portion above the point of entrance into the right auricle, is bound to the sheaths of the pulmonary arteries and bronchi —in other words, to the root of the lung. Above this, by means of the fascia surrounding the vena cava superior, the lateral fornix is indirectly attached to the superior aperture of the thorax. The pericardium has also a loose areolar attachment to the œsophagus and descending portion of the thoracic aorta. Sibson's fascia roofs in the cervical aspect of the pleura, and affords a surface of implantation for a number of fascial and muscular fibres which keep the pleura in position. It has no direct action in supporting the diaphragm.

The foregoing evidence, I believe, is sufficient to demonstrate that the cervico-thoracic fascia, continuous below with the pericardium, forms one of the chief supports of the diaphragm. Additional proof may be adduced, in the cadaver, by exercising downward traction on the diaphragm, when the sides of the neck will be indrawn with each downward pull, and a similar effect may be noted on throwing the diaphragm into contraction by the application of boiling fluids to its under surface.

B. *Inferior or Abdominal Supports of the Diaphragm.*—The diaphragm is supported from beneath by the abdominal viscera, themselves kept in place by the tonic contraction of the abdominal muscles. In proportion as this tonus is impaired, one or more of the viscera gravitate downwards and become displaced, the most extreme condition being seen in some cases of enteroptosis. Taken in order from above downwards and forwards the inferior supports are :—

a. The liver, with its falciform, coronary, and lateral ligaments.

b. The inferior vena cava, which acts as a strong support, indirectly through the liver, in the posterior surface of which it is imbedded. Faure (54) has shown that a weight of from 27 to 28 kilograms is required to pull down the liver when all its supports excepting the vena cava have been divided, whilst 30 to 40 kilos. were needed with all the connections intact.

c. The stomach and intestines, which constitute an air-cushion on which the solid viscera, especially the liver, are supported. They are themselves retained in position by tonic contraction of

d. The muscles of the anterior abdominal wall.

G.—LEVEL OF THE DIAPHRAGM.

A. *Post Mortem.*—From an investigation (8) of eighty cases from the dissecting and post-mortem rooms I find the average highest point of the dome in the cadaveric position of expiration to be situate on the right side at the level of the upper border of the fifth rib in the mid-clavicular line, on the left side in the mid-clavicular line at the lower border of the fifth rib.

B. *Intra Vitam.*—Orthodiagraphic measurements (55) in adults show that in moderate expiration the average position on the right side is at the level of the fourth intercostal space, or less frequently a little internal to the junction of the fourth rib with its cartilage on the left side on a level with the upper border of the fifth rib at its costo-cartilaginous junction. The right dome is found most often between the seventh and eighth thoracic spinous processes, the left between the eighth and ninth, whilst the central tendon lies a little above the tip of the eighth. Posteriorly the lower margin of the diaphragm is opposite the twelfth thoracic spine. Anteriorly the level of the central tendon is a little above, or corresponds with, the meso-metasternal articulation (56) (junction between gladiolus and ensiform; *vide* Fig. 4), according as to whether the diaphragm is highly arched or not, whilst posteriorly it is opposite the body of the eighth thoracic vertebra.

H.—ABSOLUTE RANGE OF MOVEMENT OF THE DIAPHRAGM.

The average adult range of movement between deep inspiration and deep expiration is 30 mm. on the right side, and 28 mm. on the left. In adult males the diaphragmatic movement is greater, being 34 mm. on the right side, and 32 mm. on the left. The average adult movement in quiet respiration is 12.5 mm. on the right side, and 12 mm. on the left. From these results of orthodiagraphic investigation in 100 healthy cases I find that the movement in quiet respiration is approximately equal on the two sides, whilst in deep breathing the excursion is for the most part slightly greater on the right side than on the left. In the diagnosis of pathological conditions the movement in deep respiration is the important one to consider (57). In quiet breathing the average descent of the central tendon is 16 mm.

I.—THE COSTO-PHRENIC PLEURAL REFLECTION.

Without mention of this important structure a description of the diaphragm would be incomplete. Elsewhere (58) I have described its nature and function. Here I will merely observe that it is formed by the meeting of the costal with the diaphragmatic portion of the pleura, its function being to bind, as it were, the diaphragm to the chest-wall and so to resemble, in point of mechanical advantage, the band or loop through which a muscle passes in order to change the direction of its force. Its apposed lubricated surfaces allow the diaphragm to glide easily, and thus markedly facilitate the action of this muscle.

J.—STRENGTH OF THE DIAPHRAGM.

By means of a mercury manometer Mosso (59) has found that the strength of the diaphragm is such that it raises 10 to 20 mm. Hg., the thorax 32 to 40 mm. Hg., and the two together 56 to 76 mm. Hg.

With reference to the comparative expansile power of the diaphragm and thorax, Hultkrantz (60) found in an experiment upon himself that the diaphragm accounted for 170 cc., and the costal elevation for 320 cc., out of a total of 490 cc. of air inspired.

V. ACTION OF THE DIAPHRAGM.

A.—As Tractor.

The difference in level of corresponding points on each dome of the diaphragm in its position of relaxation is fairly well balanced in inspiration by a complex movement on the part of the liver which may be resolved into three components:—

1. Descent;
2. Rotation about a transverse horizontal axis;
3. Rotation about a median vertical axis.

All three movements are of practical importance in maintaining the functional activity of the organ, and the first two can be verified by orthodiagraphic examination.

In clinical medicine I venture to think that the amount of descent of the anterior liver-border usually is overestimated, the apparent descent being greater than the real, and caused by a sliding of the liver-margin from behind forwards over the radial border of the index finger of the palpating hand.[1] On percussion the difference in dullness is less at the lower margin of the liver on inspiration than at the upper margin, and this discrepancy is explained, partly for the reason given above, partly because of the diminution in volume of the liver under compression.

In addition to the action of the fibres already mentioned, it is necessary to take into account the action of the long costal fibres which are obliquely attached from the eighth to the eleventh costal cartilages. The effect of their contraction is to pull forwards the blunt right extremity of the liver, which rotates about the spine as its axis, thus causing the sharp left extremity to be displaced backwards to the same amount as the summit of its right posterior convexity is brought forwards. Friction between the posterior surface of the liver and the right crus is reduced to a minimum by the interposition of the bursa Spigelii, within which "the Spigelian lobe of the liver descends and ascends with each respiratory contraction of the crus" ([61]). For the reason that, in inspiration, flattening of the diaphragm practically is absent, and therefore the relation of the domes to the central tendon unchanged, no rotation of the liver on a sagittal axis is possible. The slight lessening of the area of the dome which obtains in inspiration in consequence of the contraction of the muscular fibres attached round the margin of the central tendon is met by corresponding compression-shrinkage which the liver undergoes when subjected to pressure between the diaphragm and the abdominal muscles.

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[1] Under pathological conditions, especially with lax mesepaticon, a more definite and real descent can and does frequently occur.

B.—AS COMPRESSOR.

One of the chief functions which the diaphragm performs is that of a compressor of the abdominal contents. Both functionally and morphologically the triangularis sterni, diaphragm, transversalis abdominis, and levator ani are portions of one great compressor sheet, and, as such, are capable of acting in unison. The intra-abdominal pressure can be raised enormously by simultaneous contraction of these three latter muscles which in extraordinary expiration push up the diaphragm. The diaphragm, acting downwards and forwards, causes a corresponding descent of the whole of the abdominal viscera, which is resisted by the corset-action of the transversalis (Nature's stays). Contraction of the transversales causes the organs in the upper part of the abdominal cavity to be pressed upwards, the viscera in the lower part of the abdominal cavity to be forced downwards, whilst those intermediate in position are subjected to direct backward pressure against the convex surface of the spinal column and to outward and backward pressure away from the middle line into the cavities of the posterior abdominal wall. The powerful downward thrust caused by active contraction of the transversales is opposed by the levatores ani, which, exercising forward traction upon the coccyx, at the same time lift the pelvic floor with the superimposed pelvic contents, and thus lessen from below upwards the long diameter of the abdomino-pelvic cavity. The development of the powerful transversalis is directly due to the assumption of the upright position, for, although the homologues of the levator ani usually can be recognised, yet this muscle, as it exists in man and some primates, is not present in the lower mammals ([62]). Thus combined action of the above muscles compresses the abdomino-pelvic viscera, aids in the evacuation of bladder and bowel, and influences the circulation of blood and lymph.

C.—AS COMPRESSOR AND TRACTOR.

Effects upon the Circulation of Blood and Lymph.

The heart, pericardium, root of lung with the pulmonary vessels, and great vessels of the neck are all depressed by descent of the central tendon which is induced by the inspiratory pull of the crura. When the muscle relaxes they rise. The part of the aorta nearest the heart is most loosely attached, and therefore descends most, the transverse portion next, and the descending portion least, owing to its passage behind the crura and its fixation to the vertebral column. In addition to downward movement rectification of the arch also takes place, the ascending aorta being to some extent straightened and stretched. Owing to the arrangement of the fascial layers the negative pressure is enabled to act at best advantage in promoting venous flow. The aspiratory force put into action by enlargement of the thorax, extension of the vertebral column, and descent of the diaphragm, is of considerable moment; in fact, so great is the effect produced that the pumping action of the diaphragm has been likened to that of a second heart. With each inspiratory descent blood is sucked out of the thin-walled veins into the right side of the heart, and the flow through the lungs at the same time accelerated. Blood is also sent back to the right heart by rise of intra-abdominal tension, which causes compression of the splanchnic veins.

That in the normal monkey and man gravity exerts but little disturbing influence upon the circulation, and that the circulation is largely dependent upon the integrity of the vaso-motor mechanism has been conclusively demonstrated in an important paper by Leonard Hill (63). This integrity, in turn, chiefly rests upon the sustaining power of strong abdominal muscles (64). If this power fails, visceroptosis, partial or complete, results, since the contraction of the diaphragm, meeting with less and less resistance, tends to force downwards and forwards the abdominal contents, with consequent progressive and often grave obstruction to the circulation.

The liver, spleen, and stomach are compressed directly between the diaphragm and abdominal parietes, and thereby the circulation through these organs is considerably assisted. The kidneys are compressed indirectly also through the medium of the colon. Hilton (65) drew attention to the value of active respiration and exercise; and in a footnote Mr. Jackson quotes Oliver Wendell Holmes: "Every squeeze upwards of the liver" (in walking, rowing, or riding) "must send a squirt of venous blood through the inferior vena cava into the closely contiguous right auricle, whilst every downward movement draws open the same vein slightly in readiness for the next upward jet." In connection with the last-mentioned exercise, equally true is the saying, attributed to Lord Palmerston, that "the best thing for the inside of a man is the outside of a horse." It is the venous radicles, however, that are squeezed, and not the vena cava, which is carefully protected by its position in a hollow at the back of the liver; and we have already seen that, where it passes through the diaphragm, the foramen is rigid and incompressible.

From the abdominal organs and from the peritoneal cavity the lymph is squeezed by the contraction of the diaphragm and abdominal muscles through the diaphragm into the pleuræ and pericardium. The receptaculum chyli, filling during each relaxation of the diaphragm, is emptied by compression against the body of the second lumbar vertebra by each contraction of the powerful right crus, which thus drives on the lymph, the flow of which into the junction of internal jugular and subclavian is further aided by the above-mentioned aspiration-action of thorax and diaphragm through the thoracic and right lymphatic ducts.

D.—As Constrictor.

Action on the Digestive System.

The least mobile portion of the diaphragm, as we have seen, is situated in the neighbourhood of the vena cava inferior: next in lessened range of movement comes that part which is near the œsophageal opening. The walls of this tube are joined to the diaphragm by areolar tissue, and the œsophagus is subject to local constriction and diminution of its calibre, produced by the sphincter-fibres of the right crus which enclose it in a muscular canal. This fixation and constriction of the œsophagus at the cardiac orifice take place respectively for the purposes of facilitating and regulating the entrance of food into the stomach, contraction also preventing its regurgitation. One would naturally expect that the part of the stomach which adjoins the point of food-entry would be least liable to peristaltic disturbance, and this is indeed the case, since the stomach is directly attached to the diaphragm over a small triangular area uncovered by peritoneum which lies on the posterior surface of the cardiac orifice.

VI. NATURE OF THE RESPIRATORY MOVEMENTS.

An inquiry into the nature of the respiratory movements, especially with reference to the participation of the diaphragm therein, involves a careful study of some of the most complex problems in physiology. At the outset two important questions arise :—

1. Are the respiratory movements automatic or reflex in character?

2. Is the respiratory rhythm controlled by one centre in the medulla, or do other centres exist?

Although both of these problems have been attacked vigorously at home and abroad, endeavours to solve the difficulty as to whether the mammalian respiratory centre is reflex or automatic have been beset "with insurmountable difficulties owing to the impossibility of isolating that centre from all others, and of studying its nature." In Limulus, the king-crab, the respiratory mechanism, according to Hyde" ([66]), is governed by the branchial ganglia of the ventral nerve cord, and each ganglion which is a centre for the activities of its segment can be isolated or hemisected without interference with the segment to which it belongs. Further experiments demonstrate that these branchial ganglia are reflex, and that the expiratory movements, although they may be influenced by other factors, are dependent upon, and modified by, impulses from brain, heart, and intestinal plexuses, abdominal longitudinal muscles, and peripheral stimuli ([67]). According to Gaskell ([68]), the branchial ganglia in Limulus are comparable to the ganglia presiding over gill-movements in Ammocoetes and the hagfish, being homologous with the respiratory centres of the higher vertebrates. In the skate the respiratory centre is segmental, occupying a place intermediate between the simple segmental arrangement in Limulus, and the complex and modified centres of higher vertebrates ([69]).

Since the year 1878 various experiments have been performed by Mosso ([70, 71, 72]) with the object of finding out whether the movements of respiration are automatic or reflex. One of these is here given in detail as a sample: Nine grams of chloral were injected into the jugular vein of a dog weighing 8.500 kilos., both vagi being then divided. Artificial respiration was performed for more than a minute by means of bellows communicating with the trachea without subsequent modification of respiratory movements. Two Marey's tambours were placed at different levels on the thorax communicating by means of a Y-shaped tube with a recording lever writing on a revolving drum: another tambour was applied to the epigastrium. Simultaneous records of thoracic and abdominal respirations were obtained in this way. On suspending artificial respiration there was no change either in respiratory rhythm or movements of thorax and diaphragm. Intense artificial respiration for over a minute failed to produce apnœa. Thus the animal was found insensible to the gaseous changes in the blood which, in ordinary respiration, produce variations in rhythm. Artificial respiration was again performed twice during the experiment without causing change in respiration. Hence, from this and like experiments, one must conclude that, even after division of the vagi, respiration is still controlled, and that the changes in the blood, even during most forcible breathing, are insufficient to modify the rhythm and force of the respiratory movements, which Mosso therefore regards as automatic.

Further, carbon dioxide acts directly upon the expiratory centre for a longer time and with greater effect than upon the inspiratory centre. Carbon dioxide, administered to an animal with divided vagi, causes more active play of the abdominal and facial muscles than obtains in ordinary respiration. Hence expiration would appear to be an active process.

Psychic phenomena induce changes in abdominal and thoracic movements during attention, distraction, sleep, &c., which are instantaneous. Hence one is led to infer the existence of cerebral respiratory centres.

Difference of opinion exists as to the excitability of the respiratory centre, Mosso believing it to be variable, whilst Loewy affirms that it is constant. Breuer (73) and Hering have stated as the result of experiment that changes in the volume of the lungs influence the respiratory movements through the vagus, so that distension of the lung acts reflexly by inhibiting inspiration, and promoting expiration, while decrease in volume inhibits expiration and promotes inspiration.

Although for lower animals these results may hold good they are not to be relied on in the case of man. Moreover, along with absence of mechanical and tactile sensibility for movements of the lung, chemical sensibility in the peripheral terminations of the vagus is also absent.

Intimate relationship exists between the centres for thoracic and diaphragmatic respiration and the tonicity of the muscles employed, and the vigour and rhythm of contraction show variations synchronous with changes in the tonicity of diaphragm and thorax.

VII. NATURE OF THE RESPIRATORY CENTRES.

Recent opinions strengthen the conception that anabolism and katabolism continually take place within the nerve cells of the respiratory centres, the nutrition of the cell, through the medium of its lymph and blood supply, constituting the formative (anabolic) processes, whilst the destructive (katabolic) changes give rise to the respiratory movements. The experimental work of Luciani and Mosso shows that, although the structural equilibrium of these cells is liable to variations in degree of stability resulting from the influence of external stimuli, yet upon these the functions of the respiratory centres do not directly depend. Thus the respiratory centre may be regarded as a source of chemical energy which, by a series of combustions at regular intervals, is transformed into other forms of energy, the cell-functions being modified under the influence of extrinsic agencies. The products of combustion in all probability influence the regulator mechanism, as instanced by the marked increase in rhythm and vigour of respiration produced by carbonic oxide.

Pansini (74), studying the innervation of the diaphragm in small mammals, such as guinea-pigs, rabbits, and fœtuses of dogs and cats, in all of which the diaphragm is thin and almost transparent, has stated that, at the level of the diaphragm, quite apart from the sympathetic diaphragmatic plexus, the phrenic nerve forms with the branches of the three last intercostal nerves a complicated plexus divisible into anterior, lateral, and posterior portions, and that, in this latter portion especially, there are intrinsic ganglia, whose presence, taken in conjunction with clinical and experimental facts, explains that functional independence which the diaphragm not infrequently exhibits. By the adoption of similar formic acid and chloride of gold methods I have experimented on the same lines as Pansini, and, though agreeing with him in his description of the branching of the phrenic nerve to supply the different parts of the diaphragm, in rabbits, which were the only small mammals which I examined, so far I have been unable to verify the existence of intrinsic ganglia. Minute dissection under water of the nerves of the human diaphragm in the youth and adult reveals that the four branches into which the phrenic nerve divided towards the periphery are connected by fine filaments, and microscopic examination of the main trunk confirms the statement that it is made up of a number of irregularly disposed and interlacing bundles of nerve-fibres, an arrangement which, however, is not peculiar to the phrenic nerve. I am hopeful at some future time to proceed with these experiments, but, up to the present, have only found nodal points at irregular intervals along the course of the phrenic branches in the diaphragm, which, on being treated with chloride of gold solution and teased under the microscope, failed to yield any structure resembling ganglion-cells, and are probably localised thickenings of the sheath.

VIII. AUTOMATIC ACTION OF THE DIAPHRAGM.

In support of the view that independent action of the diaphragm exists, already a mass of positive evidence has been adduced. If intrinsic ganglia are present in the human diaphragm, to these the almost certain automatism of this muscle can be referred. Meanwhile, in the absence of any direct evidence that such ganglia occur in man, it is possible to refer the causation of the independent action of the diaphragm to one of the subsidiary cord centres. The Continental school of physiologists believe the respiratory centres to be multiple, and not confined to the vital knot of Flourens in the medulla as most British writers until recently have asserted. On the former view the centre of Flourens is probably the chief co-ordinating centre for a series placed at different levels in the central nervous system. From the cord nerves branch out on each side to the muscles which enlarge the cavity of the chest. If the phrenic nerves be divided, the diaphragm will cease to act; if the spinal thoracic nerves be divided the intercostal muscles will cease to act. Legallois (75) found that, by dividing the spinal cord below the phrenic origin in the cat, the movements of the thorax cease whilst those of the diaphragm do not, and that, by cutting the cord between the occiput and origin of the phrenics, the movements of thorax and abdomen cease simultaneously. Schiff (76) was the first to prove that, after destruction of the medulla, the diaphragm was still able to act in response to cutaneous stimulation. He further showed that the respiratory impulse descends in the lateral columns of the cord (77), and that therefore the diaphragm will contract only on that side on which the lateral column is intact. Within recent years it has been shown by Porter (78) that the respiratory impulse descending from the bulb to the diaphragm can cross to the opposite side of the cord only at the level of the phrenic nuclei. The careful observations of Brown Sequard (79) show that rise and fall of the diaphragm persist in animals whose phrenic nerve has been stimulated, and that, after death, when the thoracic movements have ceased, the diaphragm goes on contracting for some long time after every other striated muscle except the heart is motionless. Marey (80) has demonstrated that in obstructed respiration the diaphragm enters into action before the thoracic muscles, and relaxes whilst their action is still going on. In a series of experiments Bert (81) found that after (1) longitudinal section of the cord from the first to the fourth pair of cervical nerves, (2) complete transection of the cord above the first pair, and (3) complete transection below the second pair, each half of the diaphragm still contracts. Section below the third pair abolishes diaphragmatic movements. Rokitansky (82) pointed out that, when the medulla is put out of action, young rabbits to whom strychnine has been given can still perform respiratory movements. Langendorff and Nitschmann (83) discovered spinal centres apart from the medulla capable of reflex or automatic action. Christiani (84, 85) located an inspiratory centre in the third ventricle and an expiratory centre in the corpora quadrigemina. Later still Mosso (72) has shown that respiratory movements of face, thorax, diaphragm, and abdomen are mutually independent, that alternation exists between the respiratory movements of thorax and abdomen, by means of which, when the force of the diaphragmatic contraction lessens, the thoracic action increases, and *vice versâ*, that periods of intermission in the movements of the diaphragm occur while the thoracic movements continue uniformly equal, and that hiccough can produce at intervals strong contraction of the diaphragm without thoracic participation. More recently still, as mentioned above, Pansini (74) has described in lower mammals the existence of diaphragmatic ganglia, and has called attention to the rhythmical contraction of this muscle which takes place in hysteria apart from thoracic movements.

IX. TYPES OF RESPIRATION.

Although custom has sanctioned the division of respiration into two "types"—thoracic and abdominal—yet this classification is by no means exact. "Thoracic respiration" really means maximum increase in all diameters of the upper part of the thorax, and "abdominal respiration" a similar effect in the lower part of the thorax. In the former case the breathing is mainly upper costal, and in the latter case lower costal. Pure thoracic or pure abdominal respiration seldom occurs; breathing, though usually "mixed," being labelled according to the then dominant factor. Nor is it easy to draw a hard and fast line between the two groups on account of the variations and transitions in type which frequently befall. Under the stress of altered conditions, especially in young people with elastic thorax, each is capable of rapid transformation.

Accentuation of one phase may be voluntary or involuntary: with a little training pure thoracic or pure abdominal breathing may be produced at will: emotions cause changes which are rapid and involuntary. The need of deeper and fuller respiration often intervenes, greater volume of air being indrawn by a "thoracic" inspiration than by one which is solely "abdominal." In sleep respiration is shallow, and the "thoracic type" prevails. In change of type either part or whole of the remainder of the respiratory mechanism may be brought into play. Sex has a definite influence, the diaphragm and abdominal muscles being used to a much larger extent in males than in females, the chief respiratory movement in the latter, as is well known, being upper thoracic. Age-changes also bring about variation, the diaphragm becoming less functionally active with advancing years. According to Gregor (86), up to the seventh year of child-life, the abdominal or mammalian type of respiration persists: subsequently the abdominal muscles offer increased resistance to inspiratory visceral descent and the type becomes more thoracic, this change being more marked in girls than in boys.

Idiosyncrasy, habit, will-power or suggestion, and any emotion or even sudden change of thought may cause variation in the order of respiratory events.

X. EFFECT UPON THE DIAPHRAGM OF CHANGE IN POSITION.

Change in the position of the body has a considerable effect upon the tension of the resting diaphragm. In a quadruped placed in the vertical position the diaphragmatic function is almost entirely inhibited owing to the additional muscular efforts necessitated by the assumption of this unusual attitude (87). Hence experiments of this nature on the lower animals give no useful information with regard to the diaphragm. Tension influences contractility; therefore the rhythm and force of the respiratory movements are correspondingly altered. Amplification of upper costal inspiration is gradually induced by the act of lowering a man from the vertical into the horizontal position. The chest dilates and passes into a position of greater elevation. Since with this upper thoracic elevation there is coincident passive rise in the level of the diaphragm, which assumes a more expiratory position, the capacity of the thorax remains much the same. and spirometric observations in vertical, horizontal, and intermediate positions show that there is but little change in the quantity of air taken in with each breath. Hence it seems reasonable to infer the existence of an automatic regulator mechanism, which is brought into action only under the influence of mechanical stimuli, and which compensates for differences in the inspiratory movements of thorax and diaphragm. In the erect position there is less change in the tonus of the diaphragm, a fact which is partly due to the weight of the intra-abdominal viscera attached to it. Seeing that the resting position of the diaphragm in the horizontal posture is at a higher level than in the vertical position, in contraction it is enabled to act at greater mechanical advantage. During general anæsthesia respiration is often to a great extent diaphragmatic, even in healthy subjects, and the dorsal position is usually the best, provided that the head is neither flexed nor extended, and that it is kept turned to one or other side. When respiration is wholly diaphragmatic, as in very stout subjects, lessening of the work of the diaphragm is best attained by turning the patient partly or completely upon his side (88).

Intra-abdominal Pressure.

The pressure within the abdomen depends upon—

1. The pressure of the atmosphere on each point of the parietal superficies.
2. The tonus of the muscles of the body-cavity.
3. The position of the body.

The intra-abdominal pressure is subject to much variation. Usually it equals, or, more frequently, exceeds that of the atmosphere, hence the greater or less convexity of the abdominal superficies caused by the outward push of the contents: occasionally it is negative, with consequent indrawing of the belly-wall. The maximum pressures occur in individuals of strong muscular development; with weak abdominal muscles there is a tendency to negative pressure. The pressure is, as a rule, greater in males than females, and in nulliparæ than in those in whom pregnancy has occurred, the chief factor in all cases being the tone of the abdominal musculature.

XI. PRENATAL MOVEMENTS OF DIAPHRAGM AND THORAX.

It is possible that movement of the diaphragm may take place even before birth. In fact intra-uterine fœtal respiration has been described by Ahlfeld (89), who finds in obstetric literature several confirmatory references to this condition, and states that, towards the end of pregnancy, in addition to the fœtal movements of trunk and limbs, intra-uterine movements of thorax and diaphragm occur, wave-like in character and irregular in frequency (38 to 76 in the minute, the average being 61), and quite distinct from the maternal breathing, aortic pulse, and uterine contractions. A newborn child, placed in a bath of warm water, performs similar thoracic movements. If the fœtus in utero inspires, its nostrils must contain amniotic fluid, and this is found to be the case. Since, at birth, the intra-thoracic contents occupy a relatively higher position in the body than at any subsequent period, if the diaphragm enters into action, as it is said to do, before birth, this action can be only passive. The viscera are adapted for descent at birth, as evidenced by the folds into which the cervico-thoracic fascia and pericardium are thrown, and the sinuous course taken by the phrenic nerves and œsophagus. When the child is born, active contraction of the diaphragm straightens these structures, and puts them slightly on the stretch. Had the crura, on the other hand, actively contracted before birth, the thoracic contents would not have exhibited their characteristic puckered prenatal condition. Hence probably the chief share in intra-uterine respiration is taken by the thorax, the diaphragm participating only to a small extent. No contraction of the right crus of the diaphragm having yet taken place, the heart has not been subjected to the downward movement from this source which it afterwards acquires in addition to its own movements. At birth the diaphragm begins its life-work by contracting for about 2 cm. or more in downward and forward direction, and thus, simultaneously with the expansion of the lungs, puts an end to the fœtal circulation. Keith is of the opinion that, before birth, the superior and inferior limbic bands (sup. and inf. limbs of the annulus ovalis) pull on the right crus, and thus force the blood from the inferior vena cava into the cavity of the right auricle. At birth the contraction of the diaphragm closes the foramen ovale by altering the direction of the limbic bands. "Their fixed points are now defined, and when they and the tænia terminalis contract, the vestibule of the right auricle, and of course the fossa ovalis, are completely shut off from the atrium" (90). By the same contraction the ductus arteriosus is closed, and the lungs are expanded.

XII. THE DIAPHRAGM IN RESPIRATION.

A.—CONSIDERATION OF SIMULTANEOUS THORACIC AND ABDOMINAL RESPIRATIONS IN STANDING, SITTING, AND RECUMBENT POSTURES.

In order to secure a graphic record which shall give some idea of the various types of respiration, and the alterations therein produced by change of posture in man, it is necessary to take simultaneous tracings of thoracic and abdominal movements. For this purpose two healthy adult males of medium muscular development were chosen, the examination being conducted in the Physiological Laboratory of the Cambridge University. The records of the one, aged 38, will be found in Series A, tracings I., II., III.; the records of the other, aged 29, form Series B, tracings I., II., III.

In each individual a tambour was applied to the front of the chest and another to the epigastrium. To the tambours on chest and abdomen Brodie's tambours with writing levers 11 cm. in length were joined by rubber tubing in such a way as to indicate inspiration by a rise of the writing-point and expiration by a fall. Kymographic tracings were then taken, the upper line recording thoracic movements, and the lower line abdominal. The drum was set to revolve at the lowest speed but one, the time being indicated in intervals of one second.

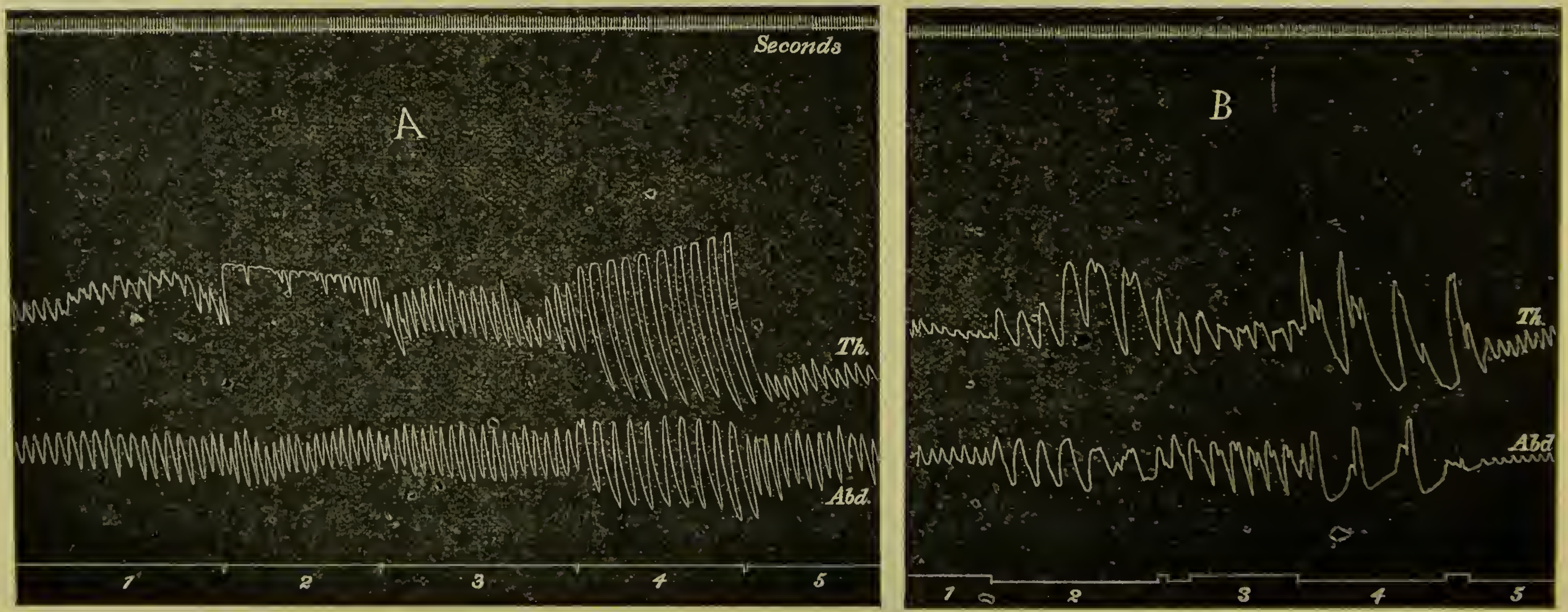
Tracing I., A and B, records respiration whilst standing.
„ II. „ „ „ „ sitting.
„ III. „ „ „ „ lying.

The Arabic numerals represent voluntary and successive changes in respiration :—

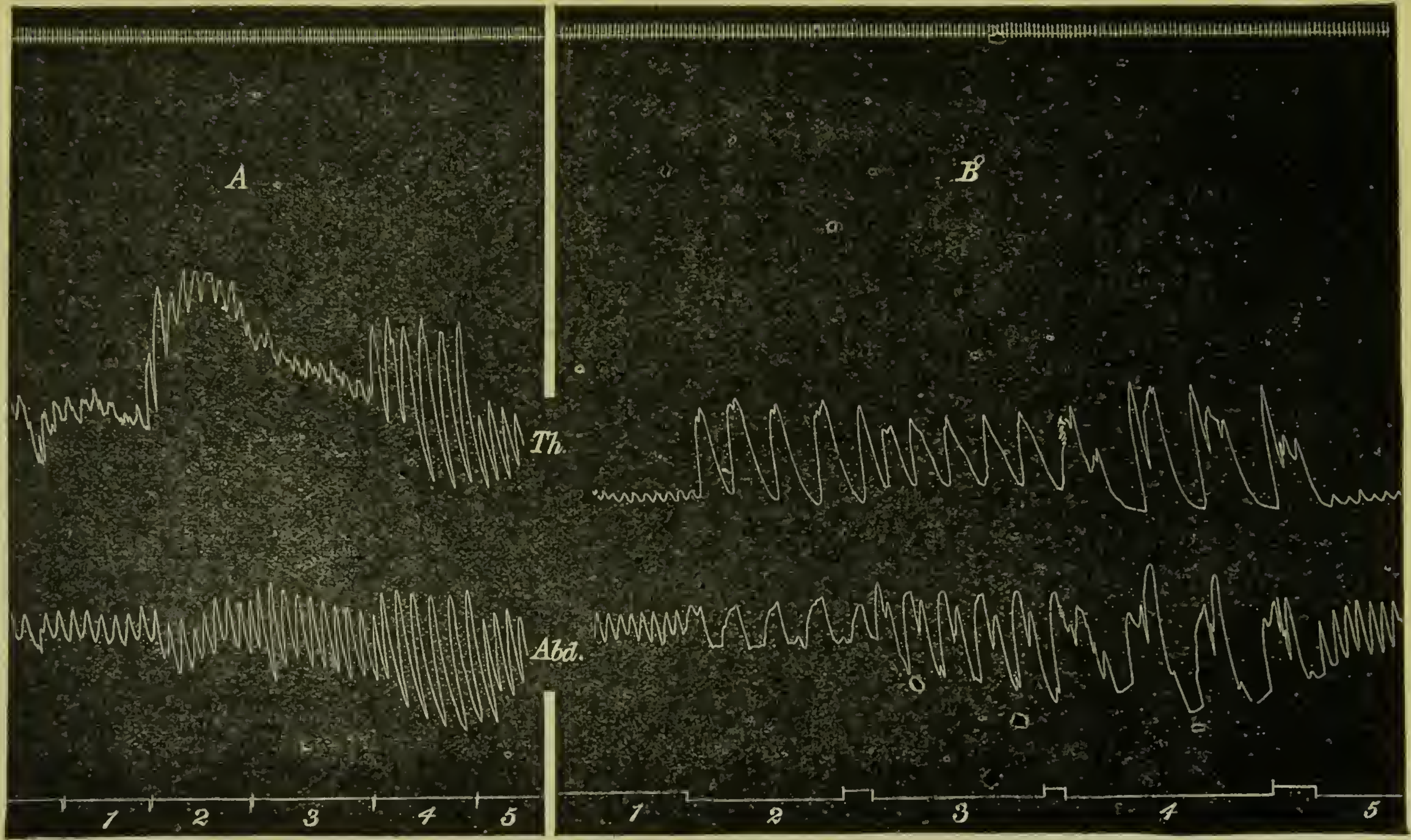
1. Ordinary respiration.
2. Moderate costal respiration.
3. Moderate diaphragmatic respiration.
4. Deepest possible inspiration and expiration.
5. Ordinary respiration.

General Characteristics of the Tracings.

Each series shows well the frequent lack of correspondence in the extent of thoracic and abdominal movements, a few contractions of approximately similar length being followed by one or two shorter ones, thus showing increase of thoracic action coincidently with decrease of diaphragmatic action, and *vice versâ, e.g.* A B, II. and III., 2, 3. This phenomenon is repeated at fairly definite intervals. In other words, the respiratory

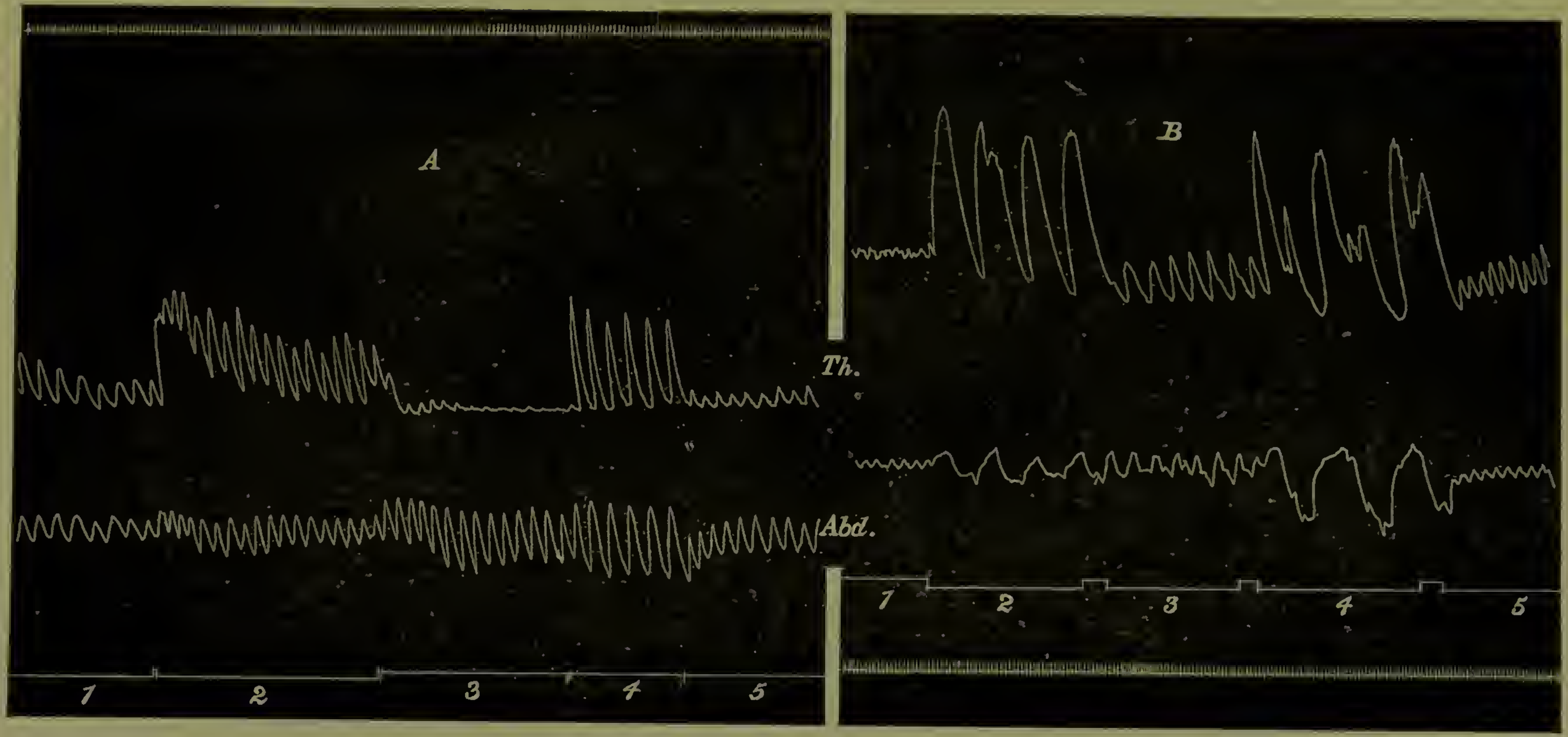


TRACING I.—RESPIRATION WHILST STANDING.



TRACING II.—RESPIRATION WHILST SITTING.

movements of the thorax, although usually proportional, do not vary directly with those of the diaphragm. Although the force of the respiration varies, the frequency of contraction remains much the same. The thorax can carry on the whole of respiration when the diaphragm is motionless, as in paralysis of the diaphragm, and both it and the abdominal muscles can function independently of the thorax. This is exemplified in a case of spinal disease recorded by Hilton (91), and in sparteine-poisoning Cushny and Matthews (92) have found that the muscles of the thorax and abdomen contract whilst the diaphragm is paralysed. In A and B I. we find the abdominal excursion in quiet breathing greater in amplitude than the thoracic, which latter exhibits a species of dicrotism, probably muscular, showing that expiration takes place in two stages and is not absolutely continuous, together with tiny undulations which may be due to the blood-pressure. The "dicrotism" becomes more marked in B 2, but the lesser waves disappear. In A and B 3, thoracic inspiration proceeds rapidly until the diaphragm has attained its maximum contraction, and then expiratory undulations with subsequent rapid fall obtain, more marked in B 3. The diaphragmatic expiration is not continuous, but occurs in two main stages. In B 4 the amplitude of the curves is marked, the first half of the upward rise is gradual, and represents the contraction of the diaphragm, the second half is sudden and caused by the contraction of the abdominal muscles (absent in A). The two phases are synchronous, for the diaphragm begins to contract before the thorax has ceased to expire. When respiration returns to the ordinary, the thoracic excursion at times exceeds the abdominal (B, I., 5), thus instancing how, within a brief interval of time, change of type can occur. Again in B, II., 3, contraction of the diaphragm happens before the thorax has finished expiring, and the diaphragmatic and abdominal portions of the inspiratory wave are well seen in B, II., 4. The most marked variations occur in B, III. Following tranquil breathing, upper costal respiration is suddenly brought into action, accompanied by slight corresponding increase in the abdominal movement A and B, 2. Not infrequently the abdomen goes on expiring after the thorax, *e.g.* B, II., and a line drawn so as to join the summits of the inspiratory curves is seen to be approximately straight, showing correspondence between thoracic and abdominal movements at the end of inspiration, whilst a line joining the lowest points of the expiratory curves is irregular. For the sake of simplicity it is convenient to regard the diaphragm in respiration as being composed of three portions, a central



Tracing III.—Respiration whilst Lying.

and two lateral, which are subject to relative variations in the amount of displacement which they can undergo; the two lateral portions, although correlated in amplitude of excursion, nevertheless under certain conditions usually pathological, exhibiting functional independence of action.

B.—MOVEMENT OF THE DIAPHRAGM.

1. *In Ordinary Inspiration.*—Inspiration is essentially a muscular act, having for its object the overcoming of resistance to expansion which is offered by the combined elasticity of lungs and thorax.

During ordinary inspiration the diaphragm enters into active contraction, and depresses the central tendon to an extent which varies with its load, with the amount of thoracic muscular action, and with the strength of the abdominal muscles. The diaphragm is the chief and most powerful muscle of respiration. In both sexes its contraction occupies a considerable portion of the inspiratory cycle; the extent of the rib-movement, even in women, not being as great as often thought, and in men, particularly in the upper thoracic region, decidedly small. At the moment when active descent of the diaphragm lengthens the vertical diameter of the thorax, this diameter apparently is lessened by simultaneous elevation of the ribs to which it is attached. Since, however, by the latter process the sterno-vertebral diameter is much augmented, so far from diminishing the inspiratory effect of the diaphragm, this elevation actually increases it.

When the diaphragm enters into contraction it becomes an active muscle of inspiration; when it relaxes and adapts itself to the changes in intra-thoracic and intra-abdominal pressure it becomes a passive muscle of expiration. The effect of the inspiratory diaphragmatic movement in increasing the diameters of the thorax is manifested in two ways:—

(*a*) In upper thoracic breathing by active contraction of the muscle, the central tendon undergoing but little alteration in position;

(*b*) In lower thoracic breathing by active contraction, the central tendon being displaced downwards and forwards.

(*a*) *Active Contraction of the Diaphragm in Upper Thoracic Respiration.*—Diagrammatically the abdominal parietes may be figured as a hollow cylindroid packed with viscera and capable of variations in surface form, the most movable portions being the area of attachment of the anterior muscles—the upper end (diaphragm), and the lower end (perineum).

Suppose now, the diaphragm being at rest, all the other muscles to exercise graduated and continuous pressure upon the contained viscera. If contraction of the diaphragm takes place, the resistance offered to its downward and forward pull will be equivalent to that produced by an incompressible cylindroid with convex ends. On this solid rod the diaphragm can make no impression, the abdominal viscera being squeezed tightly and moreover being kept taut within their capsules by the blood-pressure. The central tendon fits like a cap on the upper convex surface of the liver and is inelastic. Therefore from this as its relatively or absolutely fixed base of support the diaphragmatic fibres have to act, and the effect of their shortening, aided as it is by the simultaneous contraction of the quadratus lumborum, which fixes the lowest ribs, is to raise and expand the portion of the thorax above these to which the peripheral fasciculi are attached, and, in some cases, to evert the lower margin of the thorax.

(*b*) *Active Contraction of the Diaphragm in Lower Thoracic Respiration.*—In males the greater part of the respiratory movement is abdominal, much of the surface movement being caused by the diaphragm pushing downwards and forwards the abdominal viscera. Yet the amount of movement of the abdominal wall in itself does not bear an absolute ratio to the extent of diaphragmatic contraction, since in inspiration the reduction in size of the abdominal cavity produced by descent of the diaphragm may be counterbalanced to a large extent by widening of the lower part of the thorax, and there may be even no movement of the abdominal parietes at all. Again, in expiration, whilst the thorax narrows, the hollow of the diaphragm is considerably raised. Hence, on looking at an individual, or at graphic records of the respiratory movements, one is uncertain as to how much abdominal movement is an index of diaphragmatic contraction. Moreover, movement of the abdomen as a whole occurs when the diaphragm undergoes merely passive displacement,

Adopting for a brief moment the popular idea of the diaphragm as the septum which forms the roof of one cavity and the floor of the other, it follows that inspiratory descent enlarges the diameters of the thoracic cavity at the expense of the abdominal, whilst expiratory ascent acts in contrary manner. Owing to raising of the ribs, the diaphragm increases the horizontal thoracic diameter as well as the vertical, but the latter is the one most enlarged.

In active contraction of the diaphragm each constituent part shares to an extent corresponding with its own structure and disposition. Thus the fibrous portion is inelastic and incontractile, whilst the muscular part contracts with an effect which varies directly with the length and cross-section of its fibres, and the resistance—variable or constant—which is offered to their action. Of the muscular portion the sternal fibres are much the shortest and least active; the middle fibres of the crura are the longest and play the most active part; while the peripheral band springing from the costal margin is intermediate in length and power. This does not mean, however, that the diaphragm will be drawn down proportionately to the length and strength of muscle-tissue in particular regions, since, as stated above, the resistance of the contiguous structures in various situations is various. The function of the crura is to pull down the mediastinal structures through the medium of the pericardium, which is inelastic. Hence, although it might be thought that the posterior portion of the central tendon would move most on account of the attachment of the crural fibres to the posterior border, constituting, as they do, by far the longest and strongest portions of the muscle, yet, as a matter of fact, although its downward movement is greater than that of the anterior portion, it does not possess as much movement as the domes. Much of the energy of the crura is absorbed in swinging the liver downwards and forwards. The direction of the fibres, too, must be taken into account, the sternal fibres, which, on moving downward have assumed a more horizontal course, can only act by pulling inwards the lower end of the sternum, and have but little further action in drawing down the central tendon. "For the effective contraction of this muscle its attachment to the lower ribs is kept fixed by the contraction of the quadratus lumborum" ([93]). A link may be found to connect the active with the passive movement of the diaphragm in that this muscle by its own contraction helps to expand the lower aperture of the thorax. A condition of tonus of the abdominal muscles is necessary in order that this expansion should take place through the pushing forwards of the belly-wall in the neighbourhood of the attachment of the anterior musculature to sternum and costal cartilages.

If one watches the movement of the diaphragm in a live rabbit one cannot fail to be struck with the way in which descent of this muscle is induced by the simultaneous contraction of the powerfully acting crura. This contraction probably causes the slight depression above referred to, which is at times manifest on orthodiagraphic examination a little external to the summit of the curve when the diaphragm is acting strongly, and is, according to expectation, more common in males than females.

2. *In Ordinary Expiration.*—Expiration consists in a combination of muscular action with visceral recoil. The anterior abdominal muscles push back the intra-abdominal viscera, this action being supplemented by the potential energy accumulated through inspiratory change of position of thoracic and abdominal viscera, which, when the diaphragmatic compression is released, by reason of their inherent elasticity, tend to return to their former state, and so to raise the relaxed diaphragm. In order that expiration shall take place the diaphragm must remain passive, and in this condition is most susceptible to intra-cœlomic pressure-change, its curve, however, being maintained by the shape of the visceral surfaces above and below it, particularly by the concavity of the lung. Although the diaphragm can be pushed up, under physiological conditions it cannot be pushed down.

Simultaneously with abdominal activity decrease in thoracic capacity takes place with drooping and recession of the previously elevated sternum and ribs, depression of the latter being actively assisted by the interossei interni (94). The vertebral column resumes its original position and the head and shoulders advance. Keith (95) has stated that "the elasticity of the lungs plays only a passive part in expiration," and that "so delicate is the elasticity of the lung that artificial respiration quickly destroys it." On the other hand, Tillaux (96) remarks: "The lungs are powerfully elastic. Distend a lung, and it shrinks immediately the insufflation has ceased. This experiment shows the great resistance to insufflation. It is very difficult to break the pulmonary vesicles by blowing with all the strength of one's own lungs, for the lung-tissue though soft is very strong; so that the production of emphysema is not to be feared in artificial respiration." Probably the truth lies somewhere between these conflicting utterances. I do not, however, agree with Keith that the lung plays a purely passive part in expiration, and that its collapse "is determined solely by the muscles of respiration," although this part probably is but a minor one, a greater share in recoil being taken by the visceral layer of the pleura which is closely adherent to the lung and composed almost entirely of elastic fibres which exercise, as I believe, some considerable action in expiration. Again, with West (97), "there is good ground for believing that the contractility of the lung is not simply elastic, but is due in some measure to the muscular fibre with which it is so richly provided." I am strongly of the opinion that ordinary as well as forced expiration is an active process. In many of the lower animals expiration is accomplished mainly by the elasticity of the lungs aided by the abdominal muscles, and it is likely that the same occurs in man. François Franck (98) has found that in the earth-tortoise the pulmonary sacs are enclosed by a membrane of pleural character which possesses inherent contractility, which aids active contraction of the whole organ. Contraction of the pulmonary tissue still obtains on stimulation, even when this pleural membrane is stripped off. In birds the transverse septum plays an active part in expiration and is aided by elastic contraction of the thorax and by contraction of the abdominal muscles (99). So, too, in certain of the mammalia, *e.g.* the rabbit, whose respiration is allied to that of man, there is active contraction of the abdominal muscles. Without movement of the abdomen an animal cannot breathe properly. In other words, just as we see in other parts of the body direct interaction between opposing groups of muscles, the one group being unable to contract without corresponding lessening of resistance on the part of its opponents, so in expiration the abdominal muscles are the direct antagonists of the diaphragm. The diaphragm can only contract by overcoming the resistance of the abdominal muscles: when the abdominal muscles contract the diaphragm is temporarily inhibited. Inspiratory compression of the viscera is not thereby invalidated because tonic contraction persists throughout all periods of the respiratory cycle, and inhibition to the extent of paralysis does not occur. Similar antagonism takes place between the inspiratory and expiratory sets of thoracic muscles.

3. *In Forced Inspiration.*—In forced breathing the first portion of the inspiratory act consists of a more powerful contraction of the diaphragm than in ordinary breathing accompanied by a pushing out of the abdominal wall. But forced breathing is more than this. In the second part of the movement the chest gradually expands from below upwards until finally it assumes a position of extreme elevation. The ribs are raised, the angles which they make with the costal cartilages are opened out accompanied by simultaneous widening of the infra-costal angle. Finally, straightening of the vertebral column occurs through contraction of the erector spinæ with consequent carrying back of the head and shoulders, which are held rigid in order that the extraordinary muscles of respiration may come into play and so complete the inspiration. The position of best mechanical advantage is attained by fixation of the muscles of the shoulder-girdle. The chief enlargement of the thoracic cavity occurs

in the costo-vertebral and diaphragmatic directions. The essential differences between deep and quiet breathing are (*a*), that the lower half of the thorax does not expand to anything like the extent of the upper half, in the lowest portion expanding even less than in quiet breathing, and (*b*) that in the latter part of the act the abdominal wall ceases to advance and then actively recedes, under these circumstances the abdominal muscles acting as antagonists to the powerful spinal muscles in keeping the centre of gravity vertically above the point of support. Thus it is that the thoracic cavity enlarges chiefly in its upper part through elevation of ribs rather than by descent of diaphragm. The traction of this muscle upon the lower ribs overcomes their property of elevation, but the slight reduction in size of the thorax produced by this constriction is more than counterbalanced by the diaphragm's greater descent. Constriction takes place only during forced breathing (100), and undue narrowing is resisted by the downward pull of the abdominal muscles on the ribs and the downward push of the abdominal viscera. In rapid deep breathing the intercostal spaces tend to be sucked in. The important action of the fibres passing obliquely upwards from the seventh costal cartilage and attached to the pericardium and central tendon behind the xiphoid in pulling downwards the lung on the right side and the heart and lung on the left, has been touched upon by Sibson (100).

4. *In Forced Expiration.*—In this act the abdominal muscles play the chief part. The first event is relaxation of the diaphragm and pericardium, this being followed almost immediately by recession of the abdominal wall, changes taking place in thorax and abdomen similar to those which occur in quiet breathing. To these are superadded a vigorous contraction of the abdominal musculature, which has the effect of thrusting upwards the abdominal viscera after the relaxed diaphragm within the hollow of the thorax, and of pulling downwards the sternum and lower set of ribs, thus lessening the vertical, antero-posterior, and transverse thoracic diameters. Simultaneously, forcible lowering of the ribs as a whole is caused by strong contraction of the internal intercostals, and the whole of the extraordinary muscles of expiration are brought into play with resulting further depression of ribs and shoulder-girdle, forward movement of the vertebral column, and compression of the abdominal viscera, in which latter function the levator ani is an essential auxiliary.

SUMMARY.

The influence of respiration prevails in continuity throughout the body-cavity, and from beginning to end the act of respiration is essentially muscular. Primarily the diaphragm was concerned only with circulation; at a later date, respiratory function was superadded. Owing to its central position the diaphragm enters into associate action for a large number of physiological purposes. It is formed from the cervical portion of the transversalis sheet, and develops beneath the fourth and fifth cervical segments, subsequently, along with its chief nerve, undergoing caudad migration. Five elements enter into its composition. Homologous structures exist in vertebrata, especially among the tailed amphibians. In addition to the phrenic, the seventh, eighth, ninth, tenth, and eleventh intercostal nerves, occasionally the twelfth, supply this muscle. The four great serous cavities intercommunicate by lymph-paths through the diaphragm, which is supported from above and below. Its level and range of movement have been accurately measured by the orthodiagraph. The costo-phrenic pleural reflection, as well as acting as a link of attachment to the chest-wall, allows the diaphragm to glide easily. The diaphragm acts as tractor, compressor, and constrictor. In addition to the main respiratory centre, it is possible that other subsidiary ones exist, and that the action of the diaphragm at times may be automatic. Prenatal movements of this muscle have been described. Its tension is altered by change in position of the body. Chapter xii. deals with a comparison of thoracic with abdominal breathing in various postures, and with the movements of the diaphragm in various phases of respiration.

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